Proceedings of the United States National Museum

SMITHSONIAN INSTITUTION • WASHINGTON, D.C.

Volume 124 1968 Number 3647

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SMITHSONIAN INSTITUTION PRESS

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the United States
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The Suborders of Perciform Fishes

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Introduction

The basic concept and limits of the order Perciformes (Percomorphi) as defined by Regan (in various papers but especially 1929) seem to me to be the best yet proposed. Patterson (1964) has presented the view that the Perciformes are polyphyletic. In the same broad sense that mammals are polyphyletic (cf. Simpson, 1959) this may well be, but the particular lines of polyphyletic perciform derivation drawn by Patterson (1964) seem highly unconvincing (Gosline, 1966b). Still more recently, Greenwood, et al. (1966), have removed some of the forms here included in the perciform fishes to the separate superorders Atherinomorpha and Paracanthopterygii. This action, which seems to me to involve a confusion between convergence and inheritance, is in my opinion untenable (see below). Various people, including Regan (1936) and the present author (1962), have tinkered with the boundary lines established by Regan (1929) for the Perciformes. Of such authors, Berg (1940) made the most drastic changes. The question of whether to include certain groups in or exclude them from the Perciformes is certainly moot. Here, aside from the exclusion of the callionymoid fishes, I follow the old perciform boundaries of Regan (1929).

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The present paper is addressed to the problem of how best to arrange and classify the fishes that make up the order Perciformes. Attention has been focused on the subordinal and superfamilial levels. Families have been considered only insofar as they have been misplaced or indicate what fishes are included in a suborder or superfamily. Such formal family classifications as have been included are not original, and the sources from which they have been adopted are stated.

It has, of course, been possible to examine only a small proportion of the thousands of species included in the Perciformes. Selection of material for investigation has been made on two bases. The greatest amount of time has been spent on the most controversial groups, notably the Blennioidei. Within a group the morphologically generalized members have been investigated.

Names used throughout this paper are conventional. In no instance has an effort been made to solve nomenclatorial problems with regard either to bone or fish names.

ACKNOWLEDGMENTS.—Almost all of the work on which this paper is based has been done during tenure of a Smithsonian Research Associateship. For space and facilities in the Fish Division of the U.S. National Museum during the year 1965–1966, I am greatly obligated to the staff of that Division, especially to its Curator, Dr. E. A. Lachner. The majority of the material investigated is in the U.S. National Museum. I would like also to thank Drs. D. M. Cohen and D. W. Strasburg of the U.S. Fish and Wildlife Service and Drs. J. Böhlke and J. C. Tyler of the Academy of Natural Sciences of Philadelphia (ANSP) for the loan of specimens. Though I have benefited greatly from discussion with all of the ichthyologists in the U.S. National Museum, I would like specifically to acknowledge the help of Dr. D. M. Cohen with the ophidioids, of Drs. B. B. Collette and R. H. Gibbs with the scombroids, and of Dr. V. M. Springer with the blennioids, all of whom have been kind enough to read one draft or another of the section on the groups mentioned.

The original manuscript of this paper, submitted in December 1966, was revised and brought up to date in August 1967. Both drafts have been typed by my wife, whose assistance gratefully is acknowledged.

Material Examined

Unless otherwise noted, all material investigated forms part of the U.S. National Museum fish collections. Specimens that were examined merely for superficial characters will not be listed. Other material falls into four categories: a very few of the specimens were cleared and stained by the trypsin method developed at the USNM by Dr. W. R. Taylor; a number of forms were X-rayed through the courtesy of the USNM Fish Division; some of the skeletons in the skeleton collection

of the Fish Division were utilized; and the majority of the material listed consists of single preserved specimens, one side of which has been dissected more or less completely with or without alizarin staining. Aside from a few specimens that disintegrated during staining, the specimens, along with their dissected parts, are now back in the bottles from which they came.

Names of species are those on the USNM bottles, except in one or two instances wherein the generic name obviously was incorrect.

ANABANTOIDEI.—Specimens of *Ophicephalus* species (148517), *Anabas testudineus* (102556), and *Osphronemus goramy* (12876).

Specimens of *Nandus marmoratus* (44785) and *Pristolepis fasciatus* (107835) were stained and dissected.

One specimen of *Luciocephalus pulcher* (35737) was X-rayed.

Among comparative material, one stained and cleared (17428) and one stained and dissected (8568) specimen of *Centrogenys marmoratus* and one partially dissected *Toxotes jaculatrix* (174913) were examined.

ACANTHUROIDEI.—Partially dissected specimens of *Teuthis oramin* (195521), *Zanclus canescens* (82945), and *Prionurus sculprum* (3882).

SCOMBROIDEI.—The stained and partially dissected specimen, about four inches long, upon which the account of *Scombrolabrax* is based was loaned to me by Dr. D. W. Strasburg. The original description was checked subsequently against a series of *S. heterolepis* (USNM 187651), one of which was stained.

A whole series of tuna and mackerel skeletons in the collections of the USNM and the University of Hawaii was examined for the pineal organ.

OPHIDIOIDEI.—One X-rayed specimen of *Gadopsis marmoratus* (ANSP 81566) kindly loaned by the Philadelphia Academy of Natural Sciences. One stained and partly dissected specimen of the same species (48813).

Two stained and partially dissected specimens of *Neobythites gilli* (200553) and one of *Dicrolene intronigra* (200554).

One partly dissected specimen of *Brotula barbata* (131279). One stained and partly dissected *Lepophidium negropinna* (197144).

Among comparative material, one stained and partly dissected *Phycis regius* (190434) and one "Macruridae" (158664) were examined.

BLENNIOIDEI.—Parapercidae: one partly dissected *Prolatilus jugularis* (176470) and an X-ray of the same species (77365); X-rays of *Mugiloides chilensis* (114930), *Pinguipes brasiliensis* (83241), and *Parapercis allporti* (179797); partly dissected *P. cephalopunctata* (1430785).

Trichonotidae (sensu lato): one partly dissected *Hemerocoetes* species? (177085); one skeleton (26335) and one stained and partly dissected specimen of *Bembrops gobioides* (158132).

Cheimarrichthyidae: one stained and partly dissected *Cheimarrichthys fosteri* (198510).

Bovictidae: one partly dissected *Cottoperca gobio* (114925).

Nototheniidae: one stained and partly dissected *Trematomus pennellii* (179676) and one partly dissected *Eleginops maclovina* (77319).

Harpagiferidae: one stained and partly dissected *Harpagifer bispinis* (77282).

Trachinidae: partly dissected *Trachinus draco* (31064), *T. vipera* (39473), and *T. radiatus* (2213).

Uranoscopidae: one partly dissected *Uranoscopus japonicus* (122508)

Dactyloscopidae: one slightly dissected *Dactyloscopus crossotus* (114411).

Leptoscopidae: one slightly dissected *Leptoscopus angusticeps* (39684).

Congrogadidae: one stained and partly dissected *Congrogadus subducens* (173805).

Notograptidae: one stained and partly dissected *Notograptus guttatus* (173798).

Tripterygiidae: one stained and partly dissected *Enneapterygius etheostoma* (71528).

Clinidae: one stained and partly dissected *Labrisomus nuchipinnis* (uncataloged); one partly dissected specimen of *Clinus superciliosus* (93637).

Blenniidae: one partly dissected *Blennius cristatus* (185376); one stained and partly dissected specimen of *Runula tapeinosoma* (195704).

Bathymasteridae: one skeleton (26230) and one partly dissected *Bathymaster signatus* (111994); one partly dissected *Ronquilus jordani* (103689).

Anarhichadidae: a partial skeleton of *Anarhichas lupus* (110814).

Cryptacanthodidae: one skeleton of *Cryptacanthodes maculatus* (26512).

Zoarcidae: one stained and partly dissected *Lycodes* species? (177654); one partly dissected *Zoarces viviparus* (10065); a partial skeleton of *Z. anguillarus* (26498).

A good deal of additional material, not included in the Blennioidei, was used in delimiting it.

The Basis of Perciform Classification

The Perciformes are the largest order of modern fishes. The classification, like that of fishes in general, has evolved piecemeal over the years; nevertheless, out of the efforts of such ichthyologists as Jordan and Regan, the classification of the Perciformes (and of the higher teleostean fish orders) has developed a largely unstated but nonethe-

less real structural coherence. This basic structure is accepted here, and such changes in subordinal status as are suggested have been made with the idea of strengthening rather than altering it. A brief account of the basis of perciform classification may help to explain this.

The basal percoid fishes represent the greatest focal point of fish evolution that exists today. Some 50 families of these with thousands of species generally are recognized, and they dominate all of the richer marine fish faunas. The families are differentiated on relatively slight bases but to require any other would result in one tremendous, taxanomically meaningless, and unmanageable family. As it is, the Serranidae (sensu lato) has been tending in that direction (Gosline, 1966a).

It is assumed that from the basal percoids an adaptive radiation has taken place. Some of the lines of development have differentiated very little, in which case they are still included with the basic stock; others, considered separate superfamilies, somewhat more; separate suborders, more still; and derivative orders, most of all. The question which fish belongs in which taxon and why constitutes the subject of perciform classification. Some of the theoretical and practical problems will be discussed briefly here.

The basic difficulty is the old one of vertical vs. horizontal classifications. Stated briefly: if, in figure 1*a*, the lineages, represented by

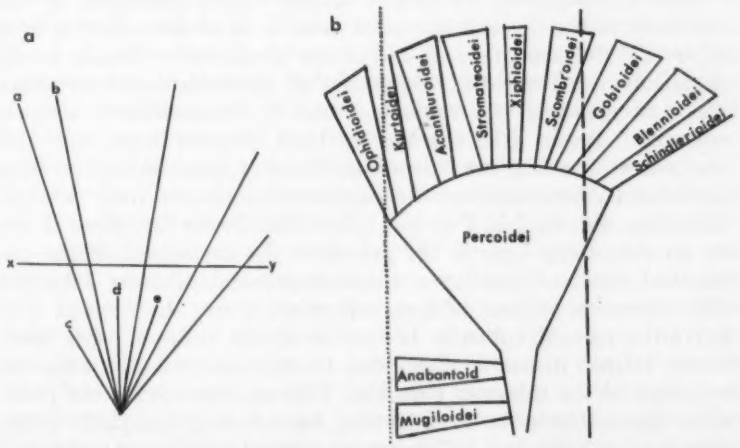

FIGURE 1.—Diagrammatic representation of perciform radiation: *a*, hypothetical (see p. 6 for lettering); *b*, with actual suborders included. (At right of broken line in *b* are those forms with dorsal and anal soft rays showing exact 1:1 correspondence with vertebrae; to left of dotted line forms have about 2+ dorsal and anal rays per vertebra; between dotted and broken lines normal ratio of 1+ ray per vertebra is maintained.)

the radiating lines, are traced back to their bases, in this case into the basal mass of percoid families, then how does one distinguish them? Contrariwise, if a line *XY*, representing some theoretical stage of structural development, is drawn across the radiating lines and everything below *XY* is called a suborder Percoidei, then how does one classify the parts of the radiating lines above *XY*?

Omitting from present consideration the mugiloids and anabantoids, Regan (1913), followed herein, places all of the Perciformes below a theoretical line *XY* in the suborder Percoidei. Matsubara (1955, 1963), following the lead of Jordan and others, adopts what is probably a more consistent approach and divides the areas both above and below *XY* into separate divisions; e.g., the Percina, Chaetodontina, Carangina. As far as I can determine, there are no concrete morphological criteria for the separation of the more basal groups, and a decision as to which of the basal percoid families should be assigned to which section has to be made on a largely intuitive or authoritarian basis. Furthermore, I feel no intuitive assurance that such a group as the Chaetodontina is not an assemblage of similar-looking but unrelated fishes. It may well be that when other and sharper tools are devised for investigating the relationships of percoid families (see, e.g., Freihofer, 1963) elimination of the line *XY* and the basal suborder Percoidei will prove feasible. For the moment, however, recognition of a central group Percoidei seems preferable.

Such a recognition, as already noted, causes difficulties in the treatment of the percoid-derivative taxa. If all of the radiating lines below *XY* (for example *c*, *d*, and *e*) are considered to belong to the single suborder Percoidei, then should all the individual lines above *XY*, however close (for example *a* and *b*), be considered separate suborders? Regan (1929) seems to have adopted essentially this course in recognizing the Siganoidea (Teuthidoidea) as distinct from the related Acanthuroidea, the Scombroidea distinct from the Trichiuroidea, etc. In this, I do not follow him. In the first place, I can see no compelling logic in the procedure. In the second, it has the practical result of creating a tremendous basal suborder Percoidei with numerous splinter offshoot suborders. Here, the concept of a derivative percoid suborder is that it should contain fishes more closely related to one another than to any other fishes outside the boundary of the suborder Percoidei. This concept admits the possibility that a derivative suborder may have been polyphyletic at the time it crossed the line *XY*. In practice (fig. 1*b*) it has the effect of combining certain of Regan's (1929) suborders.

Another problem of perciform classification is that of determining which lineages should be recognized as derivative suborders rather than as full orders. Many factors have a bearing on this question.

One is logical consistency. The callionymoids are a case in point. I believe that the callionymoids, like the gobiesocids, are notothenioid derivatives. Thus, unlike the other suborders recognized herein, the callionymoids would seem to be derivatives of derivatives of the percoids. To be consistent, therefore, they should not be placed in parallel with the other suborders recognized here but either should be included in the notothenioids or be removed from the Perciformes entirely. Of these alternatives, I prefer the latter. From the point of view of classification, the callionymoids then would have a position analagous to that of the Tetraodontiformes (which seem to have arisen from the percoid suborder Acanthuroidei).

In general, recognition of a group as a separate superfamily, suborder, or order is based on degree of morphological differentiation, precedent, and the size of the group under consideration. As to the last factor, the generally accepted dictum "that the size of the gap [between units] be in inverse relation to the size of the unit" (Mayr, 1943, p. 139) has been adopted. Thus, the large group Scorpaeniformes is considered herein a separate order from the Perciformes, though the known differences between the two units are not great (cf. Berg, 1940; Matsubara, 1953). Conversely, though the above dictum militates against small units, the complete elimination of certain small perciform suborders does not appear feasible at the present time. Thus, to combine the Kurtoidei, containing but a single genus, with any other perciform suborder would seem to abrogate phylogenetic principles. The same is true of the Schindlerioidei. Again, I have come to the somewhat reluctant conclusion that the Istiophoridae, Xiphiidae, and Luvaridae bear no real relationship to the scombrid fishes and must, at least provisionally, be placed in a separate suborder by themselves (see p. 28).

Finally, there arises the question of how to draw the line *XY* in figure 1*a*. One could draw such a line with a view to creating a definable basal suborder Percoidei. This would leave bits and pieces of radiating lineages outside the line *XY* to be tucked away in one suborder or another as decorously as possible. In practice, the line *XY* has been drawn with an eye to creating coherent derivative suborders. In figure 1*a*, therefore, *XY* should have been drawn as a zigzag line, dipping more or less deeply into the basal Percoidei at different points. In practice, then, the Percoidei contains all those perciform fishes that do not belong to some other suborder. The Percoidei presumably contain related fishes, but defining it morphologically in positive terms is difficult.

With regard to the derivative suborders, as knowledge increases, more and more structurally transitional forms between these and the basal Percoidei become known. Thus, to a greater or lesser extent,

Scombrolabrax (see p. 33) closes the structural gap between the percoids and the scombroids, *Gadopsis* (see p. 26) that between the percoids and the ophidioids, and a new family for which only a provisional notice has so far been given (Haedrich, 1967b) is stated to be intermediate between the percoids and the stromateoids. With such gaps being filled in, the separation of perciform suborders into neat, precisely definable pigeon holes becomes increasingly impossible.

The classification of the Perciformes to suborder adopted here is as follows:

Order Perciformes
- Suborder Mugiloidei
- " Anabantoidei
- " Percoidei
- " Kurtoidei
- " Acanthuroidei
- " Ophidioidei
- " Stromateoidei
- " Xiphioidei
- " Scombroidei
- " Gobioidei
- " Blennioidei
- " Schindlerioidei

"Protopercoid" Suborders

Though the great majority of modern perciform fishes belong to to the basal suborder Percoidei and its derivatives, there are two groups that at least may have developed from a "protopercoid" stock, namely the Mugiloidei and Anabantoidei.

The main, and only significant reason for considering this possibility is that the Mugiloidei always and the Anabantoidei often lack a direct articulation between the pelvic bones and the cleithra. This condition suggests the subabdominal pelvic position of prepercoid orders. Various interpretations are possible, however, and I am not sure which one is correct. First, as already suggested, the Mugiloidei and/or Anabantoidei may have evolved from a protopercoid stock in which a direct connection between the pelvics and cleithra had not yet developed. A variant of this hypothesis, again postulating a protopercoid ancestry for the Mugiloidei and/or Anabantoidei, would be that in the protopercoids, as in the berycoids, the pelvic-cleithral relationship remained variable, a more or less fixed articulation between the two elements only becoming established at the percoid stage of development. Under this thesis, the Mugiloidei would represent the nonarticulated aspect of protopercoid inheritance, whereas in the Anabantoidei the whole gamut of protopercoid pelvic variation still would be represented. Conversely, it may be, as Dollo (1909) has suggested, that the lack of a pelvic-cleithral articulation in the

Mugiloidei and in some of the Anabantoidei represents a secondary loss; certainly such a loss has occurred in such other percoid derivatives as the Stromateidae, Tetragonuridae, Gempylidae, and Trichiuridae (Regan, 1909a).

Because of the possibility that the Mugiloidei and Anabantoidei diverged from a protopercoid stock somewhat ahead of the other existing Perciformes, they will be dealt with first. Whether these two suborders, however, are considered as "protopercoid" (fig. 1*b*) or percoid derivatives is of no great moment for overall Perciformes classification.

Suborder Mugiloidei

The suborder Mugiloidei, as understood herein, contains the Polynemidae, Mugilidae, Sphyraenidae, Atherinidae, and phallostethoid families. Rosen (1964; and *in* Greenwood, et al., 1966) recently has removed the Atherinidae and phallostethoid families to a separate order Atheriniformes of the superorder Atherinomorpha. This order and superorder I believe to comprise three unrelated groups—the exocoetoids, the cyprinodontoids, and the atherinoids—all of which are adapted basically to living at or very close to the water surface and, consequently, have developed numerous features in common. The question of an atherinid-cyprinodontoid relationship has been discussed widely in recent years (e.g., Hubbs, 1944; Rosen, 1964; Greenwood, et al., 1966; and Foster, 1967). I have nothing to add to or subtract from what I have said already on the subject (1961b, 1962, 1963). Alexander (1967) recently has discussed the jaw structure of the two groups.

In an earlier paper (Gosline, 1962), I advocated the exclusion of the Mugiloidei from the Perciformes as a separate order, largely because of the consistent lack of a direct articulation between the pelvic girdle and the cleithra. At that time, I was unaware of the whole range of variation in this characteristic that occurs in the Anabantoidei. Because of the doubt thrown on the character of the pelvic-pectoral articulation by the anabantoids, as well as on other grounds (Freihofer, 1963), it seems advisable to return the mugiloid fishes to the Order Perciformes.

Suborder Anabantoidei

The suborder Anabantoidei, as recognized herein contains the Ophicephaliformes and Anabantoidei of Berg (1940) and Liem (1963), and the Luciocephalidae (Liem, 1967). The morphological divergence among these three groups is not contested. It seems to me, however as it did to Regan (1909b), that they are related more closely to one another than to any other fishes. They hold in common three morphological features that are highly peculiar among acanthopteran fishes:

a suprabranchial air-breathing organ, a gas bladder that extends posteriorly well behind the body cavity, and teeth usually present on the parasphenoid. With regard to the last feature, Liem (1967, p. 108) describes the parasphenoid of *Luciocephalus* as toothless, but according to Regan (1909b, p. 768) there are "two or three minute teeth on the parasphenoid." It may be that in the Luciocephalidae the presence of parasphenoid teeth is a variable feature, as indeed it is among the ophiocephalids and anabantids (sensu lato). Additional suggestions of a relationship among the three groups are their freshwater, Old World distribution, centering in southeast Asia, and their nest-building and/or oral-incubating proclivities. It seems most unlikely that all these features are the result of convergent evolution from independent origins.

As already noted, the pelvic girdle of some of the Anabantoidei is remote from the cleithra (*Ophicephalus*=*Channa*, *Anabas*); in others, it articulates directly with the cleithra in typical percoid fashion (*Betta*, *Colisa*, *Trichogaster*). Furthermore, in *Ophicephalus* the pelvic fin consists of six segmented rays. If the outermost pelvic rays of *Ophicephalus* represent the usual percoid pelvic spines transformed back into soft rays, such a secondary regression is only represented elsewhere, to my knowledge, among the Pleuronectiformes (Hubbs, 1945).

Among the anabantoids are found two seemingly atavistic characteristics. One, discussed at length by Liem (1967), is the presence of a mental ossification that closely resembles the gular plate of elopoid and earlier fishes. My own belief is that the mental ossification of *Luciocephalus* is not a true gular plate. The other characteristic is the parasphenoid teeth already mentioned. Aside from two other percoid families (see below), teeth on the parasphenoid are not found in the Teleostei above the elopoids. Why they should reappear in the anabantoids and two other percoid families I do not know, but again it seems to me that a postulate of reappearance is preferable to one of inheritance.

In searching for possible anabantoid relatives, one is led naturally to the two percoid families that also have parasphenoid teeth: the Nandidae and Pristolepidae. The "bite" provided by the parasphenoid dentition of *Pristolepis* is quite different from that of *Nandus* (which resembles that of *Ophicephalus*), just as that of *Ophicephalus* differs from the parasphenoid apparatus of the anabantids (sensu lato). Aside from the parasphenoid dentition, *Nandus* and *Pristolepis* appear to be rather normal percoids, lacking such specialized anabantoid features as the accessory air-breathing organ and the backwardly extended gas bladder. They do bear certain features, however, suggesting an anabantoid relationship. First, all of these fishes have an expanded auditory bulla on the cranium. Second, *Ophicephalus* (fig. 2*a*),

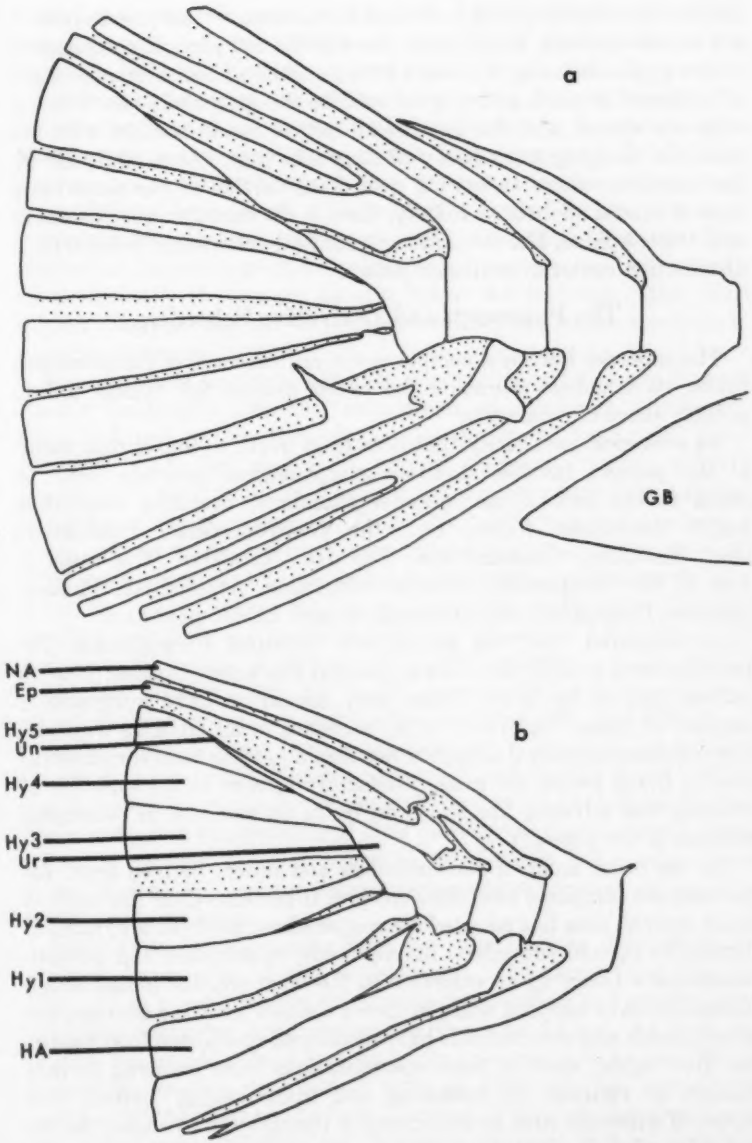

FIGURE 2.—Caudal skeletons: *a*, *Ophicephalus* species; *b*. *Pristolepis fasciatus*. (Ep=epural, Gb=gas bladder, Ha=hemal arch, Hy=hypural, Na=neural arch, Un=uroneural, Ur=urostyle.)

Anabas, and *Pristolepis* (fig. 2*b*) hold in common certain pecularities of the caudal skeleton. In all three, there is the full percoid complement of five hypurals (using Nybelin's [1963] system of counting); these are all subequal in width and splayed out like the spokes of a fan. There is only one epural, and the last hemal arch is not in contact with the urostyle. (Judging from X-ray photographs [e.g., Liem, 1967, fig. 9], *Luciocephalus* seems to have a specialized version of the same basic type of caudal structure.) Finally, there is the fact that the Nandidae and Pristolepidae, like the Anabantoidei, are freshwater fishes with a distribution center in southeast Asia.

The Percoidei and Derivative Suborders

The suborder Percoidei comprises the central mass of the perciform fishes; its members dominate the richer marine fish faunas today, notably those of coral reefs.

An ecological peculiarity that is at least worth noting is that many of the percoid families that, on morphological grounds, seem to stand at the base of the suborder contain or comprise euryhaline and/or freshwater forms; e.g., the Centropomidae, Percichthyidae, Kuhliidae, Centrarchidae, Percidae, Nandidae. The same is true of the "prepercoid" families Mugilidae, Atherinidae, Phallostethidae, Ophicephalidae, Anabantidae, and Luciocephalidae.

As compared with the presumably ancestral Beryciformes, the percoids seem to differ in no one important character (Gosline, 1966b); rather, judging by living forms, they appear to have integrated a number of minor features in what amounts to an advance over the Beryciformes in general adaptiveness. Again judging from the observation of living forms, the most satisfactory answer to the question of wherein this advance lies seems to be in an increase in swimming abilities in the percoids.

On the other hand, if the suborders and orders derived from the percoids are compared with the Percoidei, it becomes clear that each of these derived taxa has adopted some specialized mode of life; thus, of derivative percoid suborders, the xiphioids, scombroids, and schindlerioids have taken up an existence in the open sea, the gobioids and blennioids have adopted a life in direct contact with the bottom, the acanthuroids and stromateoids have developed specialized food habits, etc. But, again, most of these specializations have involved further changes in methods of swimming and maneuvering. Indeed, this aspect of existence runs so continuously through the evolution of the percoids and their derivatives that it seems well to take it up by way of an introduction to these groups.

The adult percoids are mostly maneuverers living close enough to the bottom to use it for protection but not maintaining direct physical

contact with the bottom (at least during the day). Though the defensive armature of percoids is less extensive than that of most living berycoids, the percoids seem to have provided the pelvic spines with a firmer base in the development of a direct pelvic-cleithral attachment. In bringing the pelvics forward under the pectorals, the percoids also seem to have increased their ability to maneuver. Harris (1938) showed that acanthopteran pectorals are so constructed as to give an upward thrust to the front of the fish when erected for the purpose of turning or stopping and that erection of the pelvics at the same time offsets this. In this respect, the pelvics seem to counteract the pectorals more efficiently if they are directly below the pectorals rather than behind them, as they are in lower fishes and still, to some extent, in most Beryciformes.

For the paired fins to be effective in stopping or turning, a forward speed ("headway") must have been generated previously. This is usually developed by the vertical fins and the body. Among the lower percoids, the forked caudal fin, a basal teleostean feature, plays a large role. Gero (1952) has shown that, for a swimming fish, a forked tail shape is the most efficient. From this basal type, found in such a lower percoid as *Roccus* (=*Morone*), two divergent lines of development have occurred. One is carried to its extreme in the Scombridae. Here, the widely forked fin has a short, high, relatively stiff blade firmly attached to the caudal skeleton at the end of a slender caudal peduncle. This type provides great power and speed, but it has its limitations. Harris (1953, pp. 26, 27) stated: "Tails of this type are found in fishes which are fast *continuous* swimmers (scombroids); if a sudden burst of speed from a standing start is required, the angle of attack of this type of tail would be too high and the tail would 'stall'." At the opposite extreme is the rounded caudal that has been developed again and again in percoids and their derivatives. Such a caudal shape not only provides a better "getaway" mechanism but seems to be a more efficient (or perhaps accurate) propulsive force at slow speeds and in enclosed areas.

Aside from caudal shape, there are other factors that affect the forward locomotion of the percoids and their derivatives (fig. 3). Thus, when a fish becomes either very deep-bodied or very elongate, the potentiality for rapid locomotion seems to be lost. At both extremes, the importance of the caudal fin as a source of forward thrust diminishes. Such a deep-bodied form as *Chaetodon* has a relatively long posterior border to the body, covered by the soft dorsal and anal fins, and a short, brushlike tail. In moving forward, it flaps the whole rear portion of the body, of which the tail is only an insignificant part. The end point in such a line of development is of course the tetraodontiform *Mola*, which has no caudal fin at all.

Elongate perciform fishes usually move forward by undulation, but this may be by two very distinct methods. In one, the fish holds its body more or less rigid and undulates the dorsal and anal fins only. In these forms, the dorsal and anal soft fins tend to be long and the fin rays to be closely spaced (i.e., two or more per vertebra), inserted basally on a sort of ball and socket axis, and with well-developed musculature. Locomotion by means of fin undulation seems to provide precision of movement rather than speed and enables the fish to move backward or forward with almost equal ease. Such a method of locomotion has been developed frequently among the lower teleosts; e.g., gymnarchids, gymnotids, probably halosaurids and macrourids, and the Syngnathiformes. It occurs, however, only in the ophidioids among the Perciformes (fig. 1*b*), and in the Tetraodontiformes.

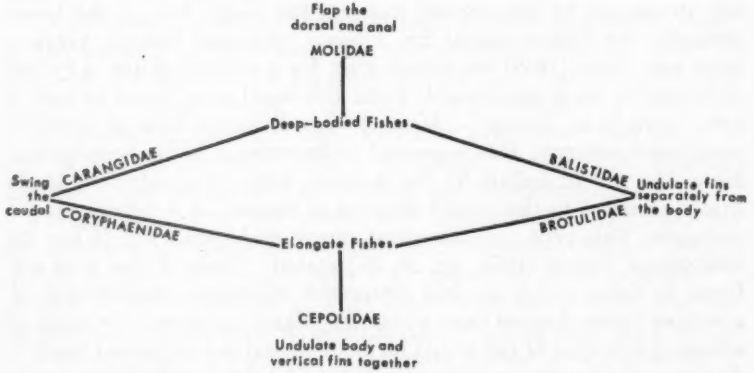

FIGURE 3.—Diagram of certain types of forward motion in the perciform fishes and their derivatives.

The other, more usual method of locomotion among elongate perciform fishes and their derivatives is for the fish to undulate its body and fins together. Here, the vertical fins tend to coordinate their structure as well as movement with that of the body, the relationship between soft dorsal and anal fin rays and vertebrae becoming 1:1. Generally, also, the number of vertebrae in such fishes is increased over the basal percoid number of 24 or 25. This development of a 1:1 ratio between soft fin rays and vertebrae in elongate perciform fishes occurs again and again (fig. 1*b*). Sometimes it occurs in free-swimming forms like the Cepolidae or Schindleriidae, but more frequently it develops in bottom-resting forms.

Whereas the great majority of the lower percoids and, for that matter, of lower teleosts, live constantly in midwater, i.e., off the bottom, a great many adult percoid derivatives have taken up a life in direct contact with the bottom, making only short dashes to obtain food or to avoid enemies. Some of the various percoid derivatives that have adopted this habit are the Blennioidei, Gobioidei, Scorpaeniformes, Pleuronectiformes, Gobiesociformes, and many Lophiiformes. The fin requirements of such forms are in many respects almost opposite to those of a swimming fish. An account of them can be deferred best to the section on the suborder Blennioidei (see p. 48).

Of the suborders among the Percoidei and their presumed derivatives, there are some for which I can add little or nothing to existing knowledge. It seems well to deal with these first, leaving until last those suborders to which the major portion of the present investigation has been devoted.

Suborder Percoidei

For purposes of the present paper, the superfamily (division) classification of Regan (1913, p. 112) will be accepted, except that his Gadopsiformes, Nototheniiformes, Callionymiformes, and most of his Trachiniformes have been removed and, following Norman (1929), the Chiasmodontoidae have been added. Here, Regan's Gadopsiformes are included in the Ophidioidei; the Nototheniiformes and most of the Trachiniformes have been placed in the Blennioidei; and the Callionymiformes have been taken out of the order Perciformes. The only family of Trachiniformes retained in the suborder Percoidei is the Opistognathidae, and this seems to belong in the superfamily Percoidae, close to the Acanthoclinidae. The Trachiniformes of Regan, thus, is abolished.

Suborder Kurtoidei

This suborder consists of a single genus. The anatomy of this peculiar fish has been described by de Beaufort (1914). I can add only that, in six specimens of *Kurtus indicus* examined, five had 15 and one had 14 branched caudal rays; de Beaufort and Chapman's (1951, p. 82) statement that the suborder has the "Caudal with 17 divided rays" seems to be in error.

Suborder Schindlerioidei

This is another perciform suborder based upon a single isolated genus. The fish is neotenic, but its peculiar caudal supporting structure seems to be unique among fishes of any stage of ontogenetic development (Gosline, 1959). The most recent of the varied suggestions concerning the relationships of *Schindleria* is that it might have evolved from something near the ammodytoid *Hypoptychus* (Gosline, 1963).

Suborder Stromateoidei

No examination has been made of any stromateoid by the present author. A recent review of the group, however, has been provided by Haedrich (1967a).

Suborder Gobioidei

Certain of the families formerly placed in the blennioids have been moved to the Gobioidei by me (Gosline, 1955), but I have nothing to add to that paper.

Suborder Acanthuroidei

The zanclids, acanthurids, and siganids (teuthidids) herein are considered members of a single suborder. The relationships among the three groups, to my knowledge, have not been disputed. The question merely is whether the siganids represent a sufficiently aberrant offshoot of the acanthurid stock to warrant a separate suborder. Starks (1907) was in doubt about the matter. From the overall view of perciform fishes taken in this paper it seems preferable to consider the siganids as one of the two superfamilies in the suborder Acanthuroidei.

The primary specialization of these fishes seems to be the development of a nipping type of jaw structure. Gregory's (1933, pp. 279–283) analysis of this structural complex and the relationships of these fishes appears to me to be entirely correct. He raises what seems to be the only important taxonomic question regarding the group; namely, whether or not it should be removed entirely to the Tetraodontiformes, which it foreshadows.

In this connection, the "prepalatine" bone (Starks, 1907, 1926) of the Siganidae (Teuthididae) warrants brief mention. In the siganids, as in the Tetraodontiformes, the upper jaw, instead of being protrusile as in most percoids, rocks in and out on the tip of the palatine as a fixed point. In the Tetraodontiformes, the whole palatine may become attached rigidly to the cranium and remain free from the rest of the suspensorium. In the siganids, a somewhat different system has been developed to accomplish the same end. The palatine bone has become divided into two parts, with the rear portion attached to the rest of the suspensorium as usual. The front portion, i.e., the "prepalatine" bone, however, has developed as a separate element from the rest of the palatine and has developed a firm attachment to the inner surface of the expanded nasal bone above and of the lacrimal below. The nasal in turn has a rigid, sutured attachment on the front of the cranium.

Suborder Ophidioidei

The suborder Ophidioidei (treated as an order by Mead, Bertelsen, and Cohen [1964, p. 580] without comment), as generally understood, contains the fishes included in the families Brotulidae, Aphyonidae, Ophidiidae, Pyramodontidae, and Carapidae. To these I add the family Gadopsidae for reasons dealt with below.

The suborder may be defined as follows: pelvics, when present, of one or two filamentous rays on each side, originating ahead of the pectoral fins; dorsal and anal long, without spines except in *Gadopsis*, the rays more numerous than the vertebrae between them; one or more of the first few ribs usually expanded.

To the end of the last century, the ophidioids, along with the gadoids, blennioids, and other fishes with anterior pelvics, generally were placed in an assemblage known as "Jugulares." In 1903b, Regan concluded (p. 460) "that the Blennioid fishes [in which Regan at that time included the ophidioids] are modified Acanthopterygii, but that the Gadoids have originated from some less specialized stock, and that the absence of non-articulated fin-rays, the large number of rays in the ventrals, and the lack of direct attachment of the pelvic bones to the clavicles, taken together must be regarded as primitive characters." Between 1903 and 1966 (Greenwood, et al., 1966) this separation of the gadoids from the blennioids and ophidiods generally has been accepted.

In 1903b, as noted, and again in 1912d, Regan included the ophidioids in his perciform suborder Blennioidea. In 1929, however, he segregated them as a separate perciform suborder "Ophidioidea." The later allocation appears to me to be correct.

The clarity of the distinction between the percoids and the ophidiods, however, is obscured considerably by the Australian genus *Gadopsis*, a morphological intermediate usually placed among the percoids but herein assigned to the ophidioids.

In my opinion, the basic specializations of the ophidioid fishes lie along two probably interrelated lines. One involves locomotion and the other sensory systems. The presumed nature of these will be discussed before dealing with general characters.

In the basal percoids (see p. 5), there are somewhat more fin rays than vertebrae, but the relationship is indeterminate (François, 1959). *Gadopsis* shows a fairly typical condition, with 28 soft dorsal rays whose pterygiophores extend downward over 25 neural spines and with 18 soft anal rays under 14 hemal spines (in the X-rayed ANSP specimen). The other ophidioids, instead of going the usual way of elongate percoid derivatives in developing an exact 1:1 relationship between soft dorsal and anal rays and vertebrae, have

developed an approximately 2 : 1 ratio between rays and vertebrae (fig. 1*b*).

Specimens of *Brotula multibarbata* in the Honolulu aquarium, though they remained with the body curved and in contact with the substrate during the period I was able to observe them, continually passed undulations along the free portions of the dorsal and anal fins. Suggestions of similar fin undulations are found in the observations of living brotulids by Whitley (1935) and Dawson (1966). This is not to say that all brotulid locomotion is carried on by fin undulation alone, for all brotulids can doubtless undulate the body in coordination with the fins and probably do when greater speed is needed. Certainly such coordination occurs in ophidiids (Herald, 1953; and Briggs and and Caldwell, 1955) and carapids (Arnold, 1956).

Phylogenetically, the argument regarding ophidioids herein advanced is not that they all swim in a manner very different from, say, the zoarcids (which have a 1 : 1 fin ray to vertebra relationship), but that their capability for independent fin undulation has led toward a morphological endpoint contrary in direction to that at which the basal percoids (with about 1.1 or 1.2 fin rays per vertebra) almost have arrived, and in a direction that has been followed by relatively few other percoid derivatives. Consequently, this development (of an approximately 2:1 fin-ray-to-vertebra ratio) in ophidioids appears to be systematically significant.

With regard to the sensory peculiarities of the ophidioid fishes, it seems to me that these are basic and that most, if not all, of the other ophidioid specializations are secondary to and related to them. Because of this, certain structural complexes that are not in themselves strictly sensory will be included in the discussion here.

Morphologically, one of the peculiarities common to all brotulids, ophidiids, *Gadopsis*, and certain gadids, e.g., *Urophycis*, is the development of the pelvic fin into one or two well-developed filaments originating more or less far forward. Functionally, the pelvics of brotulids and ophidiids have not been studied beyond the few preliminary observations of Herald (1953) and Briggs and Caldwell (1955). The function of the *Urophycis* pelvics, however, has been the subject of an excellent recent investigation by Bardach and Case (1965).

With regard to behavior, Bardach and Case (1965, p. 198) wrote in part:

> Fishes swimming along the bottom ordinarily direct their [pelvic] fins forward, with the branches spread apart to an angle of up to 45°, the entire fin sweeping from slightly forward of the snout back toward the flank (Fig. 5) [their figure]. Each fin encompasses an arc of approximately 120° ahead and to the side of the fish. Upon touching a morsel of food with a fin tip, the fish often has to back up to veer down and ingest what it found.

Although, as just mentioned, observations on living brotulids and ophidiids are only preliminary, there are two pieces of circumstantial evidence beyond gross pelvic morphology that suggest these fishes use their pelvics as *Urophycis* does. One piece of evidence is that the ophidiids, at the expense of considerable elongation of the cleithra, have brought their pelvics forward under the chin and, hence, nearer the mouth. The other is that the brotulids and ophidiids, like *Urophycis* and gadoids in general, have developed a direct route of innervation for taste perception in the pelvic fins. As Freihofer (1963, p. 141) has noted, in these fishes, the pelvic branch of the ramus lateralis accessorius "passes anterior to the base of the pectoral fin and lateral to the cleithrum and the pectoral actinosts." This does not occur in *Gadopsis*, which retains the inherited and, for fishes with anterior pelvics, circuitous nerve "route of passing down the postcleithra and then turning and coursing anteriorly en route to the distant pelvic fin" (loc. cit.).

There is, I believe, a close relationship between the method of locating food by means of pelvic filaments, as noted by Bardach and Case, and the jaw structure of brotulids, ophidiids, *Urophycis*, and, for that matter, polynemids (which presumably locate food by means of pectoral filaments). In all of these fishes, the food items are detected under the fish rather than ahead of it, and, in all, the mouth is inferior. In all also, such premaxillary protrusion as occurs extends the upper jaw vertically downward or even downward and slightly backward (rather than forward as in most percoids); the premaxillary pedicel is short and vertical, or it even extends up and somewhat forward. Finally, there is a peculiar development of a muscle to the maxillary that Rosen (1964; and *in* Greenwood, et al., 1966) called a levator maxillae superioris.

In *Merluccius*, which differs from most gadoids in having a prognathous lower jaw, I can find no "levator maxillae superioris." That some fishes with prognathous lower jaws, however, do have a muscle of this sort is clear from the batrachoid fishes (see Rosen, *in* Greenwood, et al., 1966). For a further account of this muscle in the cod, see Holmqvist (1910) and van Dobben (1935).

With regard to senses other than that of taste in the ophidioids, morphological data suggest that the acustico-lateralis system is developed highly, olfaction is normal, and the eyes are degenerate.

In *Gadopsis*, as in other ophidioids, the lateralis system of the head lies in enlarged canals that, in the pterotic (fig. 4) and circumorbital bones, are partially or completely open, bony troughs. There is also a large median opening (mucous or sensory pit) without a bony roof on the middorsal line between the two halves of the interorbital commissure.

In one respect, the lateralis system of *Gadopsis* is specialized considerably less than that of the ophidioids. In *Gadopsis*, as in most percoids, the epaxial body musculature extends forward over the dorsal surface of the skull and attaches in part to a low supraoccipital crest. The supratemporal commissure, as in most percoids and in the gadoids, is incomplete; it extends upward on each side of the head through the lateral extrascapular and then ends blindly over the epaxial musculature noted above. In the other ophidioids, the epaxial body musculature does not extend in over the skull; there is no supraoccipital crest rising above the cranial surface; and the supratemporal commissure is complete. There appears to be, as in the northern and many tropical blennies, a medial (as well as a lateral) extrascapular that has become fused completely with the parietal bones.

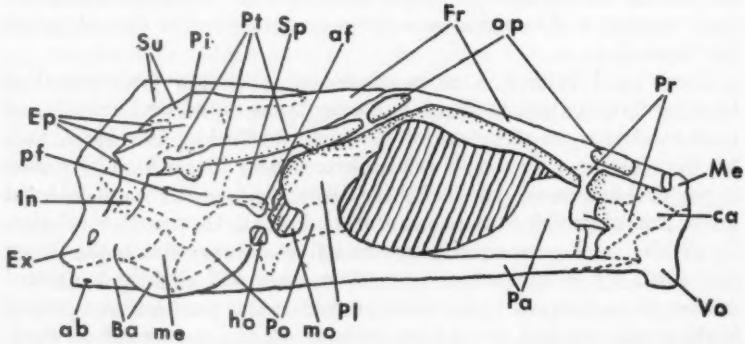

FIGURE 4.—Cranium of *Gadopsis marmoratus* (ab=attachment surface for Baudelot's ligament, af=anterior facet for hyomandibular articulation, Ba=basioccipital, ca=cartilage, Ep=epiotic, Ex=exoccipital, Fr=frontal, ho=hyomandibular opening of trigemino-facialis chamber, In=intercalar, me=membrane, Me=mesethmoid, mo=main opening of trigemino-facialis chamber, op=opening of supraorbital sensory canal, Pa=parasphenoid, pf=posterior facet for hyomandibular articulation, Pi=parietal, Pl=pleurosphenoid, Po=prootic, Pr=lateral ethmoid, Pt=pterotic, Sp=sphenotic, Su=supraoccipital, Vo=vomer).

In *Gadopsis*, as in other ophidioids, the eyes are relatively small or completely absent. In all, the eyeball seems to be capable of slight rotation or none. The eye muscles are weak and usually flabby in the preserved specimens, and there are no eye muscle canals (myodomes). The eyeball is covered by a heavy membrane. In the ophidioids this is taut over the eyeball, but in *Gadopsis* it appears to be infolded around the eyeball, perhaps permitting greater eye rotation.

The relatively small eye and weak eyeball musculature are contained in a small eye socket. This I think is associated with certain features of the skull in the interorbital region and of the brain and olfactory

nerve location. In this connection, I propose the working hypothesis that degeneration of the eye and its musculature is followed in time by the loss of the myodome and the basisphenoid and that a longitudinal trough bounded by membrane or bone and containing the anterior portion of the brain eventually will extend forward between the orbits. Extreme examples of this sort of development are found particularly in such small-eyed, broad-headed fishes as the salmonoid *Galaxias*, the gadoid *Lota* (Svetovidov, 1948), the zoarceoid *Cryptacanthodes* (Makushok, 1961a), and the ophidioid *"Dinematichthys"* (Gosline, 1953).

In *Gadopsis*, as in ophidioids and numerous other fishes, the basisphenoid is absent. The interorbital space has been encroached upon from both the posterior and elsewhere. In *Gadopsis* the anterior portion of the interorbital space is filled medianly in large part by a crest rising from the parasphenoid (fig. 4). Above and behind this crest is a V-shaped trough comprising a pair of membranes leading upward and outward from the parasphenoid crest to attachments on the lower surfaces of the frontals. At the posterior end of the orbital cavities in *Gadopsis*, the internal orbital bony walls are extended anteromedially well beyond the trigemino-facialis opening (fig. 4).

In ophidioids, as in the gadoids and other fishes, the anteromedial extension of the bony orbital rims is developed further. In *Brotula*, for example, lateral flanges from the parasphenoid meet the frontals ahead of the pleurosphenoid ("alisphenoid" of Regan, 1903b, p. 461, fig. 1A). The latter bone, now completely surrounded by other ossifications, seems to disappear completely in some brotulids.

The olfactory organ of *Gadopsis* and ophidioids seems to be developed normally. In the forms examined, the two well-separated nostrils on each side lead in over an elongate-oval rosette. In *Gadopsis*, the olfactory nerve to each rosette passes back through the lateral ethmoid and, for a short distance, through the anterior end of the orbital cavity and alongside the parasphenoid crest. About one-third of the way back in the orbits, the olfactory nerves of each side pass into the membranous trough described above. They extend posteriorly into this trough to the olfactory lobes of the brain, which project forward into the trough. (Unlike many gadoids, the olfactory bulbs of *Gadopsis* and ophidioids are at the front of the olfactory lobes of the brain; see Svetovidov, 1948, pp. 13–17.)

In the otic system of *Gadopsis* and ophidioids, there is always a more or less enlarged auditory bulla. In the juvenile *Gadopsis* dissected (106 mm SL), the wall of the central portion of this enlarged bulla is membranous (fig. 4), and the intercalar (opisthotic) has only a minute extension on it. In *Brotula*, the expansion of the bulla is

relatively slight and almost entirely comprises the exoccipital and prootic. In *Microbrotula*, the expansion is greater but comprising the same two bones. In another brotulid, *"Dinematichthys"* (see Gosline, 1953), in *Benthocometes robustus* (see Bougis and Ruivo, 1954, fig. 17), and apparently in the carapid *"Fierasfer acus"* (see Emery, 1880), the intercalar forms a part of the bulla wall.

One seems to be on fairly firm ground in associating auditory bulla expansion with some specialization in hearing though, to my knowledge, the exact nature of the association remains unknown. It is probably more controversial to attempt to relate the gas bladder peculiarities of ophidioids with hearing; however, I agree with Marshall (1965, p. 314) that there is such a relationship. In the ophidioids except *Gadopsis*, there always appears to be ligamentous tissue extending between the anterior end of the gas bladder and the anterior ribs, one or more pairs of which are modified considerably (Regan, 1903b; Arnold, 1956). In the ophidiids (Rose, 1961) and oviparous brotulids (Marshall, 1965, p. 314 quoting Courtenay, in litt.), it has been suggested that the ligaments to the forward end of the gas bladder are used in sound production.

Something should be said at this point about the Carapidae and Pyramodontidae. These families, most if not all the members of which live as inquilines in the cavities of invertebrates, generally are agreed to be related to the brotulids and ophidiids. Among the numerous features probably associated with their mode of life, however, are the loss of the pelvic fins and the development of a more or less terminal mouth, often with enlarged teeth. The other systems dealt with above seem to be essentially the same as those in the brotulids and ophidiids.

To summarize briefly the sensory systems and related structures in the ophidioids, these fishes seem to have become modified extensively in association with the development of filamentous pelvics that are used presumably as probes for finding food. Though various fishes have developed similar probes from other structures, the gadoids, ophidioids, some anabantoids, and pegasids are, to my knowledge, the only fishes that have developed filamentous pelvics of this type. By contrast, the hypertrophy of the acustico-lateralis system and the degeneration of the eyes have occurred repeatedly, especially among deep-sea forms. (Whether these features are brotulid preadaptations to or have been developed in association with a deep-sea existence has no bearing on the present argument.) The unique feature, presumably associated with the acustico-lateralis system, that the ophidioids seem to have developed is the gas bladder-rib relationship.

In the following paragraphs no attempt will be made to give any complete structural account of *Gadopsis* or other ophidioids. Regard-

ing *Gadopsis*, only those features not previously considered, in which it differs from the ophidioids, will be mentioned. In addition, in view of the recent reassignment of the ophidioids and zoarcids to the Gadiformes by Greenwood, et al. (1966), it seems necessary to discuss once again some of those features that provide the basis for believing that the similarities among these three groups are due to convergence and not to genetic inheritance.

JAW STRUCTURE.—In addition to characters already discussed, two other aspects of ophidioid jaw structure will be noted herein. First, most, if not all, of the brotulids and ophidiids retain a supramaxillary. In this minor feature, *Gadopsis* has advanced farther from the basal percoid condition, for it has no supramaxillary. Second, *Gadopsis* and the ophidioids, like most percoids, have the premaxillary subequal to the maxillary in length. In this they differ from such groups as the zoarcids, uranoscopids, and batrachoids, which often have very short premaxillaries and the much longer maxillaries to some extent included in the gape.

SUSPENSORIUM AND ASSOCIATED STRUCTURES.—The major peculiarity of the suspensorium of *Gadopsis* and the ophidioids is a trend toward the fusion of the mesopterygoid and ectopterygoid. This fusion, which seems to be a constant feature of ophidiids, pyramodontids, and carapids (see Regan, 1912d, and Gosline, 1960) occurs in *Gadopsis*. Here again, *Gadopsis* is somewhat more advanced than brotulids, in which, so far as known, the ectopterygoid and mesopterygoid are separate.

The suspensorium of the gadiform fishes and its innervation is very different from anything found in *Gadopsis*, the ophidiids, or, for that matter, in the percoid fishes. Regan (1903b, p. 464) has commented on some of the gadiform peculiarities as follows:

> Certain features of the suspensory apparatus seem to be constant throughout the suborder, and may prove to be of some importance. The head of the hyomandibular articulates with a single socket, to the formation of which the squamosal and postfrontal contribute. The entopterygoid is well developed, attached to the ectopterygoid below and in front by a vertical suture to the palatine. The palatine is attached anteriorly only to the praefrontal, and has a long maxillary process

By contrast, *Gadopsis* and other ophidioids have two more or less separate articular heads on the hyomandibular, and the mesopterygoid (entopterygoid) is attached to and forms a continuous surface with the metapterygoid and sometimes posteriorly with the hyomandibular.

The most peculiar feature of the Gadiformes is the course of the hyomandibular branch of the facial nerve. In most teleosts that have been investigated (Patterson, 1964, p. 435), as in *Gadopsis* and ophidioids, the hyomandibular branch and the main trunk of the facialis nerve exit from the cranium by separate openings, that of the hyoman-

dibular branch being posterior and more or less internal to the hyomandibular bone (fig. 4: ho). After exiting from the skull, the hyomandibular branch enters the medial face of the hyomandibular bone and passes downward within it. In the gadoids (Stannius, 1849, p. 33), the hyomandibular branch has the same cranial exit as the main facialis trunk, after which it swings backward and penetrates the front of the hyomandibular bone.

BRANCHIOSTEGAL RAYS.—The ophidioids are said to have six to eight branchiostegal rays (Regan, 1912d, p. 277); in *Gadopsis* there are seven. This is a rather high number for percoid derivatives. In the stichaeoid blennies (Makushok, 1958, p. 21), these are rarely seven, generally fewer.

PELVIC FINS AND PELVIC GIRDLE.—The filamentous fins and their presumed function in *Gadopsis*, the ophidiids, brotulids, and certain gadids already have been discussed. (Zoarcids never have filamentous pelvics.) Despite the general similarity between the pelvic fins of the Ophidioidei and certain of the Gadiformes, there are minor differences, some of which suggest different ancestries for the two groups. Thus, even when, as in the gadoid *Laemonema*, the pelvics become reduced to two main filamentous rays, there are rudimentary rays medial to these; in the ophidioids, when there is a rudimentary structure in addition to the filaments, it is a small ossicle lateral to the main rays and presumably represents a reduced spine (as in the Blenniidae and Zoarcidae). At the other extreme, however, the maximum number of soft pelvic rays in gadoids is twelve, but the ophidioids never have more than two. The pelvic fins of the Gadiformes, when present, are wide set and articulate with pelvic bones that are never attached directly to the cleithra; the pelvic fins of ophidioids, when present, are close set and articulate with pelvic bones that are usually, though not always (D. M. Cohen, pers. comm.), attached directly to the cleithra.

Freihofer (1963, p. 141) recently has noted the similarity of the ramus lateralis accessorius pattern in the gadoids, ophidioids, zoarcids, and (in litt.) nototheniids. In all of these, the pelvic branch of the ramus lateralis accessorius extends downward across the base of the pectorals instead of downward along the postcleithrum behind the pectorals and thence forward to the pelvics. But all four groups of fishes mentioned have the pelvics far forward, where the normal percoid nerve course would be highly circuitous. Furthermore, all four are groups living near the bottom, which may or do (*Phycis*, see above) use their pelvic fins to locate food. That the shorter and presumably more efficient course of the ramus lateralis to the pelvics developed independently in these groups is suggested by the fact that *Gadopsis*, herein considered to be at the base of the ophidioids, and the Bathymasteridae, at the base of the zoarcids, have a perfectly normal percoid

ramus lateralis pattern (Freihofer, 1963, p. 136). In this instance, then, I would view the similarities in nerve course as an adaptive trait that has been elicited more than once by similar circumstances.

PECTORAL.—In *Gadopsis* and ophidioids, there are four actinosts. In the Gadiformes, the number varies from three to 13. The scapular foramen of Gadiformes is usually between the scapula and coracoid; in *Gadopsis* and ophidioids, it is contained in the scapula.

DORSAL AND ANAL FINS.—It is in the structure of the vertical fins that the percoid affinities of *Gadopsis* are most plainly manifest. In that fish, there is a single dorsal fin with 10 pungent spines anteriorly, followed by 27 or 28 soft rays. Anterior to the dorsal fin, there are two well-developed predorsal bones, the anterior interdigitating between the second and third neural spines and the posterior between the third and fourth. The anal fin has three sharp, graduated spines at the front of the fin and 18 or 19 soft rays. The pterygiophores of these spines are separate, but the second is considerably enlarged and extends up in front of the first hemal arch. (One peculiarity of the dorsal and anal fins of *Gadopsis* is that its last dorsal and anal rays are not divided to the base.)

RIBS.—In *Gadopsis*, Baudelot's ligament originates on the basioccipital. There are epipleurals from the first vertebra and pleural ribs from the third. The anterior pleural ribs are enlarged only slightly, if at all. The gas bladder is large, firm walled, simple, and without special ligaments to either the ribs or skull. In all these respects, *Gadopsis* is typically percoid.

The ribs of ophidioids are modified in various ways as already noted. In one of the less-marked modifications, *Brotula* has epipleural ribs from the first vertebra and pleural ribs from the third (Regan, 1912d, p. 278). Baudelot's ligament is attached to the basioccipital; however, in *Brotula*, the first two pleural ribs are expanded, and there is a sheath of ligamentous tissue extending up and forward from the gas bladder over the anterior ribs. In no known ophidioid is the first vertebra fused to the skull.

The gadoids differ in the above features in several respects. There are never any epipleural or pleural ribs on the first two vertebrae. In most macrourids, the first vertebra is free from the skull and Baudelot's ligament, so far as known, is attached to the first vertebra. In the gadids, by contrast, the neural arch of the first vertebra is attached firmly to and its centrum completely fused into the cranium; here, Baudelot's ligament originates on the rear of the skull. Unlike ophidioids, there may be a direct connection between the gas bladder and inner ear in gadoids (in Moridae; Svetovidov, 1948), and when the gadoids have "drumming muscles," these usually are not attached to the ribs or skull (Marshall, 1965, pp. 312–313).

CAUDAL FIN AND SKELETON.—Aside from the rounded shape, the caudal fin of *Gadopsis* and its supporting structure (fig. 5*a*) seem to be of a fairly normal percoid type. There are five hypurals (counting as in Nybelin's 1963 system), one uroneural, and two epurals—all autogenous—and 15 branched caudal fin rays.

Among the brotulids, at least one member (Gosline, 1953) has 15 branched caudal rays, but there are more or less fusion and/or reduction in the caudal skeletons of all. In carapids, the caudal skeleton and fin are absent.

The caudal fin of the gadids has been the subject of much discussion. The caudal skeleton at least seems to represent a modification from a perfectly normal teleostean type (see, e.g., Barrington, 1936, and Gosline, 1964) but so reduced as to be morphologically similar to that of some brotulids.

SUMMARY.—To summarize *Gadopsis*, this fish seems in many respects to present a mosaic of characters, some percoid and others ophidioid. In the sense organs and associated structures, *Gadopsis* seems to have developed most of the basic peculiarities of the ophidioids: it has the anteriorly located, filamentous pelvics, the subterminal mouth and jaw structure, the at least partially reduced eyes, the expanded auditory bullae, and the troughlike sensory canals of the head. In the following features, however, *Gadopsis* retains the percoid condition rather than the more advanced ophidioid type: the ramus lateralis innervation of the pelvics, the incomplete supratemporal commissure, and the simple gas bladder without special relationships to the anterior ribs.

In fin structure, aside from the pelvics, *Gadopsis* shows a generalized percoid rather than the ophidioid condition. There are pungent spines at the front of the dorsal and anal, three in the anal, with the pterygiophore of the second extending in front of the first interhemal. There are two predorsal bones. The caudal fin has 15 branched rays and five autogenous hypurals. Finally, the dorsal and anal soft ray relationship to vertebrae is percoid and does not show the crowding of the rays found in ophidioids.

In a few minor characters, *Gadopsis* is more specialized than at least the more generalized ophidioids. It has no supramaxillary, and the entopterygoid and ectopterygoid are fused. Perhaps into this category should be added the fact that *Gadopsis* is a freshwater fish.

The question arises as to whether or not *Gadopsis* should be retained among the percoids or placed among the ophidioids. Zoologically, I cannot see any clearcut basis for decision. From the viewpoint of indicating the type of fish from which the ophidioids arose, *Gadopsis* and the Gadopsidae perhaps can be allocated best to the ophidioids, where the spiny-rayed *Gadopsis* would hold a position somewhat

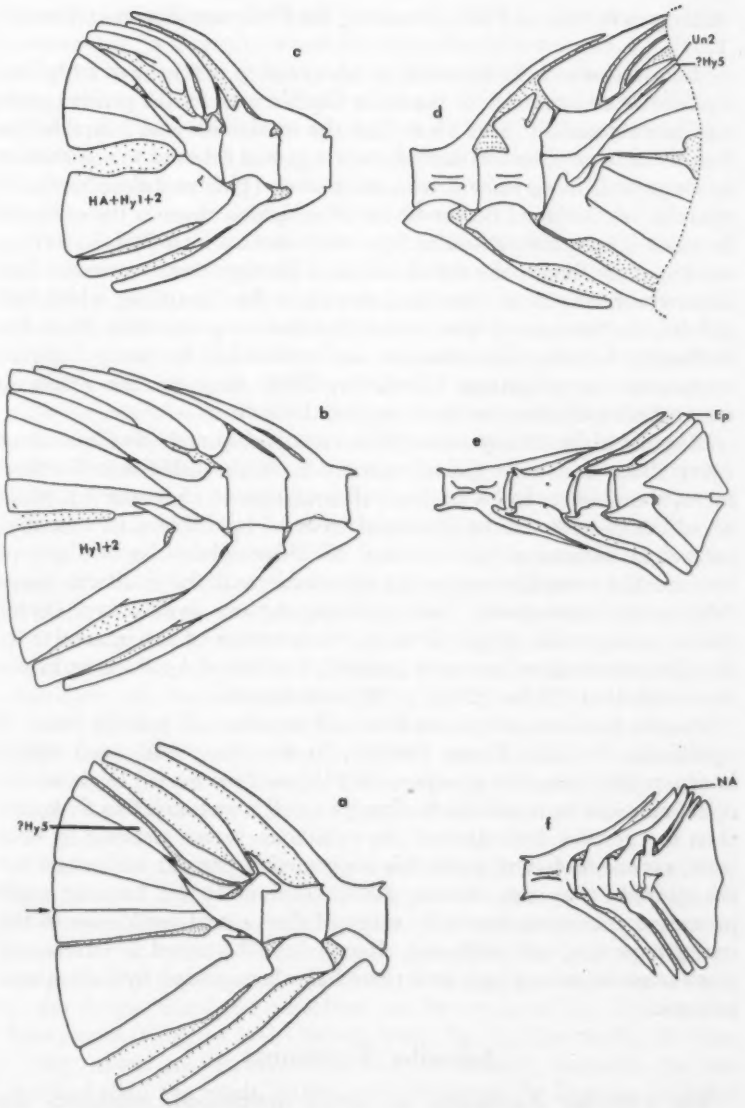

FIGURE 5.—Caudal skeletons: *a, Gadopsis marmoratus; b, Trachinus draco; c, Bathymaster signatus; d, Scombrolabrax heterolepis; e, Scomber japonicus; f, Thunnus albacares.* (*a, b, d* drawn from preserved material; *c, e, f* from dried skeletons; Ep=epural, HA=hemal arch, Hy=hypural, and NA=nural arch; broken line in fig. *d*=basal limits of cauda rays.)

analagous to that of *Psettodes* among the Pleuronectiformes (Norman, 1934).

As noted above, Greenwood, et al. (1966, p. 397), have added the ophidioids and zoarcids to the order Gadiformes. In the present paper the more generally held view that the ophidioids and zoarcids (see below) have no close relationship to the gadoid fishes or to one another is supported. In agreement with Makushok (1958 and elsewhere), the zoarcids are assigned herein to the Blennioidei, close to the stichaeid families. The ophidioids differ from these and all blennioids in having, among other things, the dorsal and anal fin rays more numerous than the vertebrae between them and, except in the Carapidae, which lack pelvics, in the one or two rayed filamentous pelvic fins. That the similarity between the zoarcids and ophidioids in ramus lateralis accessorius nerve pattern (Freihofer, 1963) may be the result of convergent evolution has been suggested above.

Regarding the fin-ray-to-vertebra relationship and the filamentous pelvic fins, some of the gadoids are similar to the ophidioids. Furthermore, there seems to be no one well investigated character by which all of the gadoids can be separated from all ophidioids; for example, no pelvic differences can be used to differentiate the two groups because the carapids among the ophidioids and the gadiform genus *Macruroides* completely lack pelvics. Again, Svetovidov (1948) placed considerable emphasis on the penetration of the intercalar by the glossopharyngeal nerve in gadoids, but this did not occur in the macrurids that Pfüller (1914, p. 76) investigated.

Despite the lack of criteria that will separate all gadoids from all ophidioids, I follow Regan (1903b), Svetovidov (1948), and others in separating these two groups widely. If, as I have tried to show, the ophidioids can be traced back through a fish very much like *Gadopsis*, then the percoid derivation of the ophidioids seems assured; by contrast, no one in recent years has suggested a percoid derivation for the gadoids (see, e.g., Rosen, 1964; Gosline, 1964). Leaving aside presumed ancestries, however, many of the central tendencies in the two groups are very different. Regan (1903b) noted a number of these tendencies long ago, and more have been added by subsequent authors.

Suborder Xiphioidei

The suborder Xiphioidei, as herein understood, comprises the families Istiophoridae, Xiphiidae, and, provisionally, the Luvaridae.

The Istiophoridae and Xiphiidae usually have been considered "a highly specialized end-stage of the scombriform series" (Gregory and Conrad, 1937, p. 23). The Luvaridae, containing only *Luvarus*

imperialis, has been allocated variously; Regan (1903a, p. 372) considered it "a most abnormal and specialized Scombroid."

A principal reason why Regan (1903a; 1909a) placed *Luvarus* among the scombroids seems to have been that in it, as in the Scombridae and Xiphiidae, "the deeply forked bases of the rays of the caudal fin are inserted nearly vertically and extend over the hypural so as to almost entirely conceal that bone, those of the upper and lower series nearly meeting in the middle line on each side" (1903a, p. 372). Additionally, in *Luvarus*, "the ossified sclerotic and broad opercular bones are typically Scombroid features" (1903a, p. 374).

In the Xiphiidae and Istiophoridae, along with the peculiar caudal ray bases noted above, the rostral structure has been considered a morphological extrapolation of the type found in the scombrids in general, most notably in *Acanthocybium* (cf. fig. in Regan, 1909a).

To the present author, it seems that all of the morphological features mentioned above may well be merely adjustments of large, powerfully swimming fishes to the requirements of hydrodynamic efficiency. (Hertel, 1966, e.g., p. 255, stresses the difference in what constitutes hydrodynamic efficiency in large, powerfully swimming animals and in small, weak swimmers.) With increase of body size and swimming speed, the role of hydrodynamic forces in the existence of the animal becomes, of course, increasingly important. It is probably significant that among the members of the percoid family Carangidae, which also contains large, powerful swimmers, almost all of the morphological characters discussed above have been duplicated. Another, at least curious, parallel in the Carangidae is that, in those forms with a high, blunt head, the premaxillary remains protrusile, as in *Luvarus;* however, in the pointed-headed Chorineminae (Suzuki, 1962, p. 147), the premaxillaries are rigid and form a beaklike structure similar to that of *Scomber*.

If, however, one excludes from consideration those features that may be related to hydrodynamic efficiency, there seems to be slight resemblance between the Istiophoridae, Xiphiidae, and Luvaridae on the one hand, and the Scombridae, on the other. In the former group, the vertebrae number from 23 to 26 (a typically percoid condition); in the Scombridae, the vertebrae are 30 or more. In *Xiphias* and *Tetrapterus* (Gregory and Conrad, 1937, fig. 5), the caudal skeleton is only about as specialized as that of *Scomber*, certainly far less modified than the caudal skeleton of the tunas. In *Luvarus*, with the fusion of the last two vertebrae, the caudal skeleton (Gregory and Conrad, 1943, fig. 7) has become modified in a different fashion than that of the Scombridae.

Probably of greater importance, the istiophorids *Xiphias* and *Luvarus* seem to guide their forward trajectory in a somewhat different

way than do the Scombridae. In the Scombridae, the route of forward trajectory seems to be controlled, at least in part, in usual percoid fashion by a combination of well-developed 6-rayed pelvics directly below the highly placed pectoral fins (Harris, 1938). In the istiophorids, xiphiids, and *Luvarus*, the pelvic fins have a reduced number of rays or none. The pectorals are low on the body and have become fixed in extended position in the adults of *Xiphias* and of the istiophorid *Istiompax indicus* (thus secondarily resembling the shark condition). In this regard, it should be noted that, in the trichiurids and in many gempylids, the pectorals are low and the pelvics reduced or absent, but such forms are relatively small, weakly swimming fishes.

Finally, the dorsal fin of the Scombridae commences well behind the head. That of the Istiophoridae and Xiphiidae originates over the back of the head. The first interneurals of *Xiphias* are shown by Gregory and Conrad (1937, fig. 3) to extend downward into the region of the skull-vertebrae articulation. In the juvenile *Luvarus* (Gregory and Conrad, 1943, fig. 38), the dorsal fin again originates far forward, but, with growth, moves back, leaving, however, a pair of large interneurals that interdigitate between the cranium and the first vertebra (Gregory and Conrad, 1943, fig. 8).

In certain respects, e.g., the 23–26 vertebrae, the Istiophoridae, Xiphiidae, and Luvaridae are more generalized than the Scombridae. That they are specialized scombrid offshoots seems an impossible conclusion, and that they are even related to the Scombridae, an improbable one.

A more difficult problem is to determine what the Xiphioidei is related to and/or derived from. Before this matter can be profitably discussed, the question arises as to whether or not the Istiophoridae, Xiphiidae, and Luvaridae are interrelated. Regan (1909a), Gregory and Conrad (1937), and others have postulated that the Xiphiidae and Istiophoridae extend back separately into Eocene times. That the two families are related more closely to one another than to any other modern family has not, to my knowledge, been questioned.

Whether or not the Luvaridae are related to the Istiophoridae and Xiphiidae is more doubtful. Certainly *Luvarus* has many features that separate it widely from all other living fishes. In mouth and snout structure, *Luvarus* differs widely from the istiophorids and xiphiids. It may be that these features provide good indications of phylogenetic relationships, but the alternative possibility at least is suggested here that the anterior profiles of *Luvurus*, on the one hand, and of the istipohorids and xiphiids, on the other, represent alternative attainments of hydrodynamic efficiency in large, strongly swimming fishes and, hence, are not necessarily of great phylogenetic significance. In any event, the Luvaridae herein are included pro-

visionally in the Xiphioidei. What appear to me to be the more important unifying elements of the Xiphioidei, as understood herein, are the following:

Vertebrae 23–26. Pelvic fins, if present, with not more than three rays. Pectorals inserted low on sides. Dorsal and anal fin rays at least somewhat more numerous than the vertebrae. Anterior interneurals interdigitating between the skull and the vertebral column. Frontal bones without a median crest (though the supraoccipital extends forward over the frontals in *Luvarus*). Nasal bones forming a rigid portion of the head skeleton (or possibly absent in *Luvarus:* see Gregory and Conrad, 1943, p. 254).

The Xiphioidei seem to have originated among the basal percoid stock, though no modern percoid group suggests any obvious relationship with the xiphioids. That the group is an old one, extending back at least to the Eocene, is well attested to by fossil evidence (though the usual attribution of the Palaeorhynchidae, with 50–60 vertebrae, to the xiphioids seems dubious).

Suborder Scombroidei

The fishes herein included in the suborder Scombroidei are the Scombridae as defined by Regan (1909a), Fraser-Brunner (1950), Collette and Gibbs (1963) and the trichiuroid fishes, i.e., the families Gempylidae (cf. Matsubara and Iwai, 1958), the Trichiuridae (cf. Tucker, 1956), and the Scombrolabracidae (Roule, 1922). The Istiophoridae, Xiphiidae, and Luvaridae, usually included in the Scombroidei (e.g., Regan, 1909a; Gregory and Conrad, 1937, 1943), herein have been removed to a separate suborder, Xiphioidei, for reasons given in the previous section.

Among the trichiuroid families, the relationship between the Gempylidae and the Trichiuridae has never, to my knowledge, been questioned. *Scombrolabrax*, discussed below, has been placed near the Gempylidae since its discovery in 1922.

Again, a postulate of relationship between the Scombridae and the trichiuroid families, particularly the Gempylidae, generally has been accepted. The only question has been whether or not the two groups should be placed together in a single suborder (e.g., Regan, 1909a) or allocated to separate suborders (e.g., Regan, 1929). It is true that the principal evolutionary trends in the two groups have been very different. That of the trichiuroids has been toward large-fanged, ribbon-shaped forms, whereas the scombrids have developed into the bulky, powerfully swimming tunas. Nevertheless, in many of what would appear to be basic structures, the trichiuroids and scombrids overlap. Indeed, the presumed gempylid *Lepidocybium* shows so many

scombrid characters (Matsubara and Iwai, 1958) that its transfer to the family Scombridae has been advocated. Conversely, the scombrid *Grammatorcynus* has a number of gempylid characters (Matsubara and Iwai, 1958). Finally, it seems that, except in a few characters, the genus *Scombrolabrax* (fig. 6), could serve morphologically as an ancestral form for the trichiuroids and, in most respects, for the Scombridae as well.

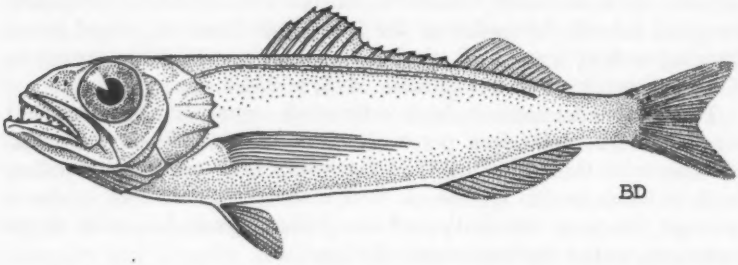

FIGURE 6.—*Scombrolabrax heterolepis:* sketch to show external appearance, based on specimen 5½ inches SL (USNM 197651) taken off Mississippi delta by the "Oregon" (drawn by Barbara Downs).

Regarding scombrid phylogeny, Kishinouye (1923) considered certain of the tunas to be so specialized as to warrant a separate order, Plecostei. This classification, though adopted by Berg (1940), was shown long ago to be based on inadequate grounds (Takahasi, 1926).

At the base of the scombrid series, Fraser-Brunner (1950) placed *Gasterochisma*. It appears to me, however, that *Gasterochisma*, which I have examined only superficially, bears at least as much resemblance to the Bramidae as to the Scombridae; if *Gasterochisma* is a scombrid at all, it is at best a highly aberrant one.

Starks (1910) seems to have been correct in considering *Scomber* as the least specialized living scombrid. Among the percoid-like characters retained by *Scomber* but lost by most or all of the rest of the Scombridae are the following:

Mesethmoid with a low median crest anterodorsally (see Allis, 1903, pl. 4: fig. 5). Intercalar not expanded on the posterodorsal face of the skull, not separating the exoccipital form the pterotic; lower limb of the posttemporal articulating with an intercalar projection that extends downward and backward from the ventral cranial surface. Premaxillaries with separate articular and ascending processes, the latter not greatly expanded (ibid., pl. 5: fig. 16). Circumorbital series of bones complete (ibid., pl. 3: fig. 4). Operculum without a smoothly rounded free border but rather with a moderately deep indention above (ibid., pl. 3: fig. 4). An anal spine present (Matsui,

1967). In the caudal skeleton of *Scomber* (fig. 5*e*), the upper and the lower hypural plates remain separate with a notch between them, and the preurostylar vertebra has no attached neural arch; by contrast, in such an advanced scombrid as *Thunnus* (fig. 5*f*), the upper and lower hypurals have fused into a single plate without a median notch and the preurostylar vertebra seems to have a well developed neural arch (fig. 5*f*: NA), though this may represent a fusion between the anterior epural of *Scomber* (fig. 5*e*) and the preurostylar centrum (cf. Gregory and Conrad, 1943, fig. 5d).

Among the trichiuroid fishes, increasing degrees of morphological specialization are shown by the series Scombrolabracidae–Gempylidae–Trichiuridae. Since no account of the osteology of the basal member of the series, namely *Scombrolabrax* (fig. 6), has ever been given, one is presented below.

The Osteology of *Scombrolabrax*

FIGURES 5*d*, 6

TEETH.—The jaw teeth are all well separated from one another, and all point more or less backward. They are in single rows except for one to three inner teeth near the midline of each jaw; these inner teeth of the upper jaw are needle-like fangs and are by far the largest in the mouth, but the inner teeth of the lower jaw are small. The outer row in each jaw is made up of well separated, sharp, distally-proximally flattened teeth; those along the sides of the lower jaw are much the larger. There is a single row of small teeth on each palatine and a V-shaped row on the vomer. Mesopterygoid toothless.

There are three patches of needle-like teeth on the upper pharyngeals of each side; the separate lower pharyngeals have similar teeth.

On the first arch are five lathlike gill rakers that, however, have spines projecting from their posterior border. The other gill rakers are in the form of low, spinulose platelets. On the rear face of the anterior arch and on succeeding arches are numerous rakers consisting of single, upright, needle-like spines (cf. Matsubara and Iwai, 1952).

There are no teeth on the hypobranchials, basibranchials, or tongue.

SENSORY CANALS OF HEAD AND ASSOCIATED BONES.—The infraorbital canal is complete and joins the supraorbital canal between the frontal and pterotic as usual. The lacrimal is a long bone that does not overlap the maxillary except far forward. It has no serrations but has the usual three canal exits along the lower surface. The first circumorbital is essentially a continuation of the lacrimal. The second circumorbital bears a very large subocular shelf that extends somewhat forward as well as somewhat back of its canal-bearing portion. Above the second circumorbital are 11 bony half rings (the medial halves) that carry

the infraorbital canal up to its junction with the supraorbital canal (three of these are slightly larger than the others and may represent the usual percoid circumorbital bones).

The supraorbital canal starts in a tubular nasal bone that is attached movably to the frontal behind it. The canal then passes back through the frontals, giving off two major lateral exits and one median. The median exit apparently represents the interorbital commissure; on each side, it passes in through a low frontal rise and opens out onto the surface of the skull on the interior slope of this rise; the opening is covered with a membrane, and there is no sign of any connection between canals of the two sides of the head.

The temporal canal extends the full length of the pterotic in a trough, open externally. The preopercular canal joins the temporal canal via a membranous tube.

JAWS.—The upper jaw is distinctly protrusile. The usual ethmoid-maxillary and palatine-premaxillary ligaments are present.

The maxillary has a long, subtriangular supramaxillary.

The premaxillary is uot beaklike. Its ascending process is nearly vertical, with the usual deep groove between it and its well-developed if low articular process over which the maxillary head rides.

SUSPENSORIUM.—The top of the interopercle and the lower portions of the subopercle and preopercle have weak serrations. There are two weak points on the opercle separated by a deep indentation; above the upper of these, the opercular edge is more or less ragged edged.

There is no metapterygoid lamina (cf. Katayama, 1959).

HYOID APPARATUS.—There are seven branchiostegals on each side, not six as reported by Roule (1922).

There is a groove along the epihyal continued forward into the ceratohyal, also one anteriorly on the ceratohyal; the grooves at the two ends of the ceratohyal are connected by a completely enclosed tunnel.

The usual gill arch bones are present.

There is a well-developed pseudobranch.

CRANIUM.—The inner face of the maxillary head rides on the side of the vomerine portion of the ethmovomerine keel. The ethmoid contributes to the keel but also has a broad, flat upper portion under and between the frontals.

Posteriorly, the frontals become slightly raised medially. Appressed against a portion of the lower surface of this rise is the "pineal organ" (Rivas, 1953). Laterally, there are two low ridges over the supraorbital canal. The whole top of the skull looks like that shown by Matsubara and Iwai (1958, fig. 5) for *Ruvettus*.

The parasphenoid is slightly arched. There is no posterior opening to the myodome.

The pleurosphenoids do not meet on the midline.

A basisphenoid is present.

The auditory bulla is swollen somewhat, with a peculiar, lateral, puffed-out area in the exoccipital. There are no soft areas on the bullae walls.

The round facets for vertebral articulation on the exoccipitals seem to be separate from each other and from the round area on the basioccipital.

PAIRED FINS AND GIRDLES.—There are four actinosts. In the wet specimen, the bottom one articulates with the cartilage over and between the scapula and the coracoid. The very long pectoral fin has 18 rays, the uppermost of which inserts below the level of the main (lowermost) opercular projecting point.

The upper, laminar postcleithrum is attached entirely to the cleithrum above. To its anterior edge is attached the lower, long sword-like postcleithrum, which runs down in back of, and has a ligament extending to, the pelvis.

The pelvis extends between and is attached tightly to the cleithra in normal percoid fashion. The pelvic bones are long and somewhat separate on the midline. They have relatively long posterior processes.

The pelvic fin has a well-developed spine and five soft rays.

AXIAL SKELETON.—Vertebrae 13+17. The first vertebra with a well-developed hemal spine is the fourteenth. Vertebrae five through 13 have parapophyses, the anterior more or less laterally directed, changing to vertically posteriorly. Pleural ribs articulate with notches in and behind the tips of the parapophyses.

In the caudal skeleton (fig. 5*d*), the urostyle extends back between the fourth and fifth hypurals (counting as in Nybelin's 1963 system), leaving the uppermost hypural alongside the two autogenous uroneurals. (The possibility that *Scombrolabrax* has only four hypurals and three uroneurals was investigated and dismissed because the lowermost of the three bones immediately above the urostyle [fig. 5: ?Hy5] ends posteriorly in a cartilaginous plate that forms a continuous edge with that of the hypurals below, whereas the upper two bones of the series, i.e., the uroneurals, do not.) There are three separate epurals and three autogenous hemal arches. The caudal rays only slightly overlap the hypurals (about as shown by Matsubara and Iwai, 1958, fig. 9).

The first dorsal pterygiophore interdigitates between neural arches two and three. There are no predorsal bones.

In the anal fin there are three close-set, graduated anal spines. The first two anal spines articulate with one pterygiophore, the third with a separate one.

INTERNAL ORGANS.—The peritoneum is black. The stomach is straight, elongate, and thick walled. There are six finger-like pyloric caeca. The gas bladder extends nearly the full length of the abdominal cavity and is rounded at both ends.

Discussion

Roule (1922, 1929) and Grey (1960) agreed that *Scombrolabrax* is related to the gempylid fishes. Both authors have noted the similarity in general appearance between *Scombrolabrax* and the gempylid genus *Epinnula*. Grey demonstrated in some detail the similarities between the peculiar lateral-line scales of gempylids and those of *Scombrolabrax*. The upper jaw structure with its long supramaxillary and its fang duplicates that of the Gempylidae as illustrated by Matsubara and Iwai (1958, fig. 3). The skull roof, as previously noted, seems to be that of the gempylid *Ruvettus*. The spinulose gill rakers again are like those of gempylids. Indeed, there seems nothing about *Scombrolabrax* that would militate against a *Scombrolabrax*-gempylid relationship.

In most instances wherein *Scombrolabrax* differs from the gemylids, it differs in the direction of the percoids. Thus, in *Scombrolabrax*, the upper jaw is protrusile, some of the opercular bones are spinous or serrate, the pelvic girdle is relatively strong and firmly attached to the cleithra, the parts of the caudal skeleton are not fused, the lateral line is simple, the lateral-line scales bear a groove rather than a completely bone-enclosed tunnel (Grey, 1960), the number of vertebrae is relatively low, etc.

If *Scombrolabrax* is included in the trichiuroid fishes and if the trichiuroids and Scombridae are combined in a single suborder, the difficulties of defining the suborder become considerably greater. The best that I can do in this regard is as follows.

The suborder Scombroidei are perciform fishes with nonprotrusile upper jaws (except *Scombrolabrax*), the postorbital members of the circumorbital ring of bones represented either by numerous small pieces or absent, the interorbital commissure of the supraorbital canals widely incomplete or lacking, the predorsal bones (Smith and Bailey, 1961) lacking, and the vertebrae numbering 30 or more.

Regarding the origins of the Scombroidei and more especially the Scombridae, these frequently have been postulated to lie in the area of the percoid family Carangidae (e.g., Starks, 1911). My own work has led to the conviction that Regan (1909a) was correct in separating the Scombridae widely from the Carangidae and that the rather numerous morphological features held in common by members of the two families (Starks, 1911) are the result of convergence. The reasons for this conclusion are as follows:

(1) In the Carangidae (see Suzuki, 1962), the supraoccipital crest always is carried forward on the frontals to the ethmoid region and

provides a source of attachment for the body musculature, which extends anteriorly along either side of it. The interorbital commissure of the lateralis canals is always complete and has a median opening between the frontals on the top of the crest.

In the scombroid fishes (including the trichiuroids), the supraoccipital crest and the body musculature do not extend forward over the head medially beyond the supraoccipital, except, to my knowledge, in *Gasterochisma*, *Scomberomorus*, and *Acanthocybium*. Other than in these genera, there is either a median open space between the frontals posteriorly or a transparent area in the frontals directly under which is an expanded "pineal organ" (Rivas, 1953). The interorbital commissure of the lateralis system is never complete (it was not located in the large skull of *Gasterochisma* examined). Except in *Scomberomorus* and presumably *Acanthocybium*, the two lateral portions of the commissure are widely incomplete on the midline; in *Scomberomorus* and presumably *Acanthocybium*, the two halves of the commissure extend up the outside surfaces of the halves of the frontal crest and open by separate exits on either side of its rim. If Rivas (1953) is correct in postulating the pineal body as a light receptor in scombroids, then the scombroids, except *Scomberomorus* and *Acanthocybium*, have a rather different system of sensory perception on the top of the head than the carangids, and the two exceptional genera would represent an incomplete return toward the carangid system.

(2) In the Carangidae, the usual five suborbital bones are present (see Suzuki, 1962), forming a typical complete circumorbital ring.

In the scombroids, the suborbital bones behind the eye are variously modified or absent. In *Scomber* and *Rastrelliger* (Allis, 1903, pl. 3; fig. 4; Starks, 1910), they form a series of flat, somewhat expanded plates that appear to be variable in number. In *Scombrolabrax*, they occur as rather numerous small ringlike ossicles (see above). In most of the other scombroids, the posterior suborbitals, along with the postorbital section of the infraorbital canal, are absent or represented by scalelike ossifications.

(3) In the Carangidae, the vertebrae are almost always 24 and never exceed 26 (Suzuki, 1962).

In the Scombridae, the vertebrae are 30 or more.

To me, a more promising area of scombroid origin among the percoid fishes is that represented today by the Pomatomidae, especially *Scombrops*. It is not so much that the pomatomids positively foreshadow the scombroids as that they appear to be more generalized percoids, lacking the rather numerous nonscombroid specializations found in the Carangidae; e.g., the median frontal crest bearing the interorbital lateral-line commissure. The Pomatomidae have the

anterior portion of the cranial roof flat or with a low arch, the interorbital commissure of the lateralis system is broadly incomplete, and the vertebrae number 26.

Suborder BLENNIOIDEI

The fishes united here under the Blennioidei form one of the most unsatisfactory suborders of the Perciformes. The blennioids are percoid derivatives that basically have taken up a mode of life in contact with the bottom. This mode of life, however, has been adopted repeatedly by percoid derivatives; indeed, it is the most successful of postpercoid developments among fishes. All of the various fishes that live in contact with the bottom have developed certain specializations in common. For one thing, all of the sense organs in which perception depends on ambient water tend to move toward the upper surface of the head and body. More important are the changes associated with locomotion. Insofar as the basal percoid must maintain at least equilibrium in a fluid environment, it is always "swimming" or at least "treading water." By contrast, a fish maintaining contact with the bottom is basically sedentary (unless it is a continuous "grazer") and swims only in short dashes from a standing start. These differences in swimming requirements are reflected in fin structure.

The problem with the bottom-living percoid derivatives is to distinguish the convergent characters associated with a life in contact with the substrate from the indicators of similar genetic inheritance. Beyond that lies the difficulty of defining groups and of separating them from the basal Percoidei.

From Linnaeus (1758) to the present, the position of the pelvic fins has formed a major basis for fish classification. The majority of the percoids and their derivatives have the pelvics more or less under the pectorals. Most or all of the derivative forms with pelvics ahead of the pectorals usually have been allocated to the Jugulares. Such a division assumes that the pelvics, once they have moved forward of the pectorals, do not return. To my knowledge, this assumption is correct. The question of how many different times the pelvics have moved forward is more difficult. The refinements in the Jugulares proposed by Boulenger (1901, 1904) and Jordan (1923) have consisted primarily in excluding from the Jugulares polyphyletic elements in which anterior pelvics had been developed independently. Jordan's (1923) concept of the Jugulares is closest to the suborder Blennioidei, as accepted here, of any classification previously proposed (see table 1).

Since the Jugulares of Jordan and Boulenger are percoid derivatives, one difficulty is to determine where the percoids end and the Jugulares start. In many percoids, e.g., the Serranidae, Cepolidae, Chiasmodontidae, and the whole series of families around the Pseudochromidae-

Plesiopidae, the pelvics are sometimes behind and sometimes in front of the pectorals. Under the circumstances, it seems impossible to adopt pelvic position alone as a basis for distinction. As an additional character, Regan (1912d) used reduction in the pelvic to four or fewer rays to separate out a group (table 1), which he called the Suborder Blennioidea. Various aspects of the artificiality of Regan's Blennioidea, however, have been pointed out by Starks (1923), Regan himself (1929), Hubbs (1952), Smith (1952), Gosline (1955), and Makushok (1958). In this paper, a different supplementary character to define the Jugulares will be adopted, namely, the presence of an exact 1:1 ratio between the vertebrae and the dorsal and posterior anal soft rays.

One result of adopting this additional criterion is to exclude from the Jugulares a number of fishes with anterior pelvics such as serranids and serranid-like families and the Opistognathidae. It also excludes from the Jugulares some almost certainly extraneous elements such as the Mastacembeliformes and Gadopsidae and three "Series" included by Jordan (1923), namely, the Brotuliformes, Ophidiiformes, and Carapiformes. If this supplementary criterion clarifies the limits of the Jugulares, it adds certain phylogenetic complications that will be noted below.

Even if the Jugulares are defined as acanthopteran fishes with the pelvics ahead of the pectorals and an exact correspondence between the dorsal and anal rays and the vertebrae, certain groups would be included that do not seem to belong there. These are the champsodontoids, the ammodytoids, the schindleroids, certain gobioids, the Pleuronectiformes, and possibly the Symbranchiformes. Of these, the Symbranchiformes can be at least technically excluded because they have no dorsal and anal rays at all. The flatfishes are set aside easily on the basis of asymmetry. The schindlerioids have no pelvics, but neither do a number of specialized Jugulares. Under the circumstances, it is easiest to exclude *Schindleria* on the basis of its fused caudal vertebrae. Among the gobioids, certain burrowing forms, e.g., *Trypauchen*, *Microdesmus*, *Kraemeria*, have anterior pelvics; these may be removed on the basis of their lack of parietals.

The champsodontoids and ammodytoids provide more serious problems. In the first place, it is not absolutely certain, in my opinion, that they should be excluded from the Jugulares. On the assumption followed here that they should be, the best means of doing so would seem to be their forked caudal fin preceded by a long, constricted caudal peduncle supported by bladelike neural and hemal arches.

The only remaining problem in defining the Jugulares is that of certain specialized groups that may well hve been derived from them. Such groups are the batrachoids and lophioids, the Callionymidae, Draconettidae, and Gobiesocidae. What the batrachoids and lophioids

evolved from is not clear to me. They are, in any event, much more highly specialized than the Jugulares in a number of respects (Regan, 1912b), and perhaps they are excluded most easily because of their rigid attachment of the post-temporal to the cranium. The Callionymidae, Draconettidae, and Gobiesocidae appear to have been derived from one of the Jugulares groups (see fig. 12). Once again, however, they are specialized sufficiently to warrant separation. They may be removed most easily by the absence of a metaperygoid.

The net effect of the restrictions outlined above is to eliminate a number of groups from Jordan's (1923) Jugulares. Such excluded groups are: the suborder Haplodoci, the series Callionymiformes, Ammodytiformes, Brotuliformes, Ophidiiformes, and Carapiformes, and the families Chiasmodontidae, Opistognathidae, Owstoniidae, Champsodontidae, and Cerdalidae. (In the families Chiasmodontidae [Norman, 1929] and Owstoniidae [Kamohara, 1935], the position of the pelvics, judging from illustrations, is somewhat variable but hardly warrants their inclusion in Jordan's Jugulares. These two families will not be mentioned further here.) The fishes in the remaining families of Jordan's (1923) Jugulares are those comprising the group to be dealt with here. These fishes may be defined as follows:

Symmetrical acanthopteran fishes with the pelvic fins, when present, inserted ahead of the pectorals. Dorsal and posterior soft anal rays exactly equal in number to the vertebrae between them. Caudal fin usually rounded; when forked, it is not preceded by a constricted peduncle supported by several fused vertebrae or by blade like neural and hemal spines. Metapterygoid and parietal bones present. Post-temporal movably attached to cranium.

Though the group herein dealt with is closest to the Jugulares of Jordan (1923), as noted above, it will be called, henceforth, the suborder Blennioidei, to bring the subordinal nomenclature into line with that usually used in fishes.

Morphological Characters

General features.—As compared with the percoids, the Blennioidei (for the families included in this suborder as herein understood see table 3) have less deep, compressed bodies. The abdominal region of the Blennioidei frequently is rather short, with the anus relatively far forward and with the caudal portion of the body always more or less attenuated. Dorsal and anal fins are low and long, usually ending posteriorly close to the outer caudal rays, and frequently extending farther forward than is usual in percoids. The caudal and pectoral fins usually are rounded. The gas bladder is generally absent in the adult.

Members of the Blennioidei that I have seen in life, primarily tropical blennies, move forward by undulation of the body and fins; even when at rest on the bottom, they maintain a sinuous body configuration.

NASAL ORGANS.—The Blennioidei are somewhat unusual in that the two nostrils have become reduced to one in two different groups. All of the cold-water blennies (Zoarceoidae) have only a single nostril on each side. The same is true of the Bovictidae, Nototheniidae, Harpagiferidae, Bathydraconidae, and Channichthyidae, though other members of the notothenioid stock, e.g., the parapercids, trichonotids and cheimarrichthyids, have two on each side. Attempts to relate nostril number to gross olfactory rosette structure have been unsuccessful. There does, however, seem to be a correlation between nostril number and geography—perhaps 90 percent of all frigid-water fishes, including Blennioidei, have one nostril on each side, whereas some 90 percent of all tropical fishes, including Blennioidei, have two.

CIRCUMORBITAL BONES (fig. 7).—The circumorbital bones have been used extensively in the classification of certain groups of Blennioidei (e.g., Regan, 1912d; Stephens, 1963; and Springer, 1964). Nevertheless, for distinguishing major groups, they must be utilized with considerable circumspection. The basal percoid pattern comprises a lacrimal and five circumorbitals, the uppermost (dermophenotic) movably attached to the cranium. The second circumorbital normally bears a subocular shelf in marine forms (Smith and Bailey, 1962). The sensory canal of the lacrimal contains several neuromast organs; that of the second circumorbital, two; the other circumorbitals have a single neuromast. Among the Blennioidei, the percoid pattern just described breaks down in many ways, though the basic trends are only two.

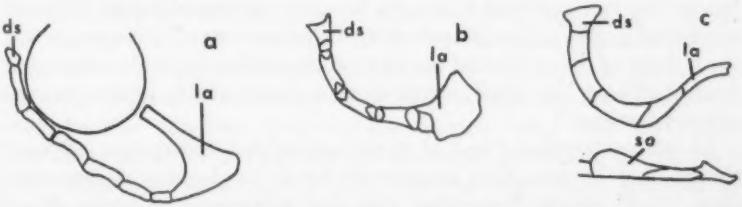

FIGURE 7.—Right circumorbital bones: *a*, *Cheimarrichthys fosteri*; *b*, *Harpagifer bispinis*; *c*, *Trachinus draco*. Lateral views, except that in *c* a top view of the anterior end of the series is shown below. (ds=Dermosphenotic, la=lacrimal, so=subocular shelf.)

The first trend, occurring in most of the notothenioid and zoarceoid series, is toward a disintegration of the circumorbital system. The first stage in such a trend is shown by the notothenioid *Parapercis* (Gosline, 1963, fig. 2a). There, the subocular shelf is missing

and six circumorbital bones are present; undoubtedly, this increase has occurred by the breaking up of the percoid second suborbital into two components, each with a single neuromast. Further change in the system may take place in three fashions. First, disintegration may come to involve the lacrimal, as apparently occurs in the zoarceoid *Lycodes*, in which the lacrimal is divided into two almost separate portions. Second, in fat-cheeked forms, the lower circumorbitals may leave the orbital border, as occurs in the notothenioid *Cheimarrichthys* (fig. 7*a*) and again in the zoarceoid *Lycodes*. Finally, the central portion of the circumorbital system may drop out entirely, as occurs in the notothenioid *Bembrops* or the zoarceoids *Lumpenus* and *Ptilichthys* (Makushok 1961b, p. 235, fig. 4).

In addition to the various stages and types of circumorbital disintegration occurring in the notothenioids and zoarceoids, there are frequent instances of a complete reversal of the trend itself. Thus, among zoarceoids, the anarhichadids have a strongly constructed, nearly rigid circumorbital chain of bones (Barsukov, 1959, pls. 7–16). Among the notothenioids, the circumorbital series forms a more or less rigid ring of bones in *Hemerocoetes* and *Harpagifer* (fig. 7*b*), and in *Crystallodytes*, this ring is made up of only three bones (Gosline, 1963).

As contrasted with the notothenioids and zoarceoids, the general trend of circumorbital bones in the tropical blennies, trachinoids, and congrogadoids is toward a strengthening of the ring and a consolidation of its elements. Again, various processes are involved. Some of these are well indicated within the single genus *Trachinus*. In *T. draco* (fig. 7*c*), which approaches the percoid condition more closely than any other member of the Blennioidei, there are a lacrimal and five circumorbitals, with a well developed subocular shelf on the second. In *T. radiatus*, the whole chain forms a rigidly interlocked series of bones; the lacrimal and what was the first circumorbital of *T. draco* are united rigidly; there is a subocular ledge running all the way around the bottom of the orbit; and the first circumorbitals have also expanded downward over the cheek, foreshadowing the condition in the "uranoscopoid families."

At the posterodorsal end of the circumorbital series, two different things may happen. One appears to be a simple loss of elements. Thus, in *T. vipera*, I can find only two circumorbital bones above that which bears the subocular shelf, instead of the three of *T. draco*. Again, among the congrogadoids, there are two circumorbital bones above that bearing the subocular shelf of *Congrogadus*, but in the related *Notograptus*, there is only one.

A different development of the uppermost circumorbital bone occurs in the topical blennies. In *Enneapterygius* and to some extent in *Clinus*,

the uppermost circumorbital retains its usual superficial position behind the orbit. But in *Labrisomus* and *Blennius*, this uppermost element becomes largely buried in the flesh and forms what appears to be a cranial bone rather than a member of the circumorbital series (Springer, 1966).

Once again, however, it must be noted that consolidation of the circumorbital series is not a universal feature in the tropical blennies, congrogadoids, and trachinoids. Indeed, in the clinid blenny *Exerpes asper*, the circumorbital chain is widely incomplete, being represented anteriorly only by an isolated lacrimal (Springer, 1955).

JAW APPARATUS.—There is no supramaxillary in the Blennioidei.

In forms with relatively long premaxillary pedicels, there seems to be two kinds of jaw protrusion. In one, represented by *Congrogadus*, the pedicels are stout and affixed firmly to the toothed portions. In such fishes, protrusion of the upper jaw may be great, but there is little possibility of expanding the gape laterally. A different system occurs in most trichonotids and in certain of the tropical blennies. Here, the premaxillary pedicel is hinged at its base with the result that the distal ends of the premaxillaries can expand outward at the same time the whole bone is protruded forward.

In the zoarceoids especially but also in the unrelated gobiesocid and batrachiform fishes, the toothed portion of the premaxillary is relatively short, with the maxillary extending well out behind it. Indeed, in such a zoarceoid as *Anarhichas*, it cannot be said that the maxillary is excluded from the gape.

OPERCULAR AND HYOID APPARATUS.—Opercular armature is uncommon in the Blennioidei.

As in other bottom fishes, water tends to be expelled from the upper portion of the gill cavity. Among many of the Blennioidei there is a special valve for this purpose (Makushok, 1958, pp. 20, 21, fig. 8). By contrast, the gill openings usually are restricted more or less below, with the gill membranes attached to one another across the isthmus or broadly attached to the isthmus. The trachinoids and the notothenioid families Trichonotidae (sensu lato) and Bovictidae are exceptional in having the gill openings extending far forward. The trachinoid fishes (Gill, 1907) and at least some trichonotids bury themselves up to the eyes in sand or mud. Baglioni (1908) has shown that *Trachinus* and *Uranoscopus*, at least, pump water over the gills by sliding the branchiostegal membranes up and down over the cleithral region. Inasmuch as the branchiostegals of these fishes and of such trichonotids as *Crystallodytes* (Gosline, 1963) are largely covered by the operculi, this method of breathing must cause a minimum of disturbance in the surrounding sand or mud.

Lycodapus, generally placed among the zoarceoids, is another fish with the gill openings extending far forward, but the relationships of this fish seem open to question.

Another feature that may be associated with wide gill openings is the branchiostegal ray number. Thus, in most Blennioidei, there are six branchiostegal rays, but in the Bovictidae and frequently in the Trichonotidae, there are seven. Among the zoarceoids, however, the Anarhichadidae, with the gill membranes broadly joined to the isthmus, also have seven. Makushok (1958, p. 21) considers the condition in anarchichadids to represent a secondary increase.

SUSPENSORIUM (fig. 8).—The suspensorium develops various modifications among the Blennioidei, but it is difficult to evaluate these phylogenetically.

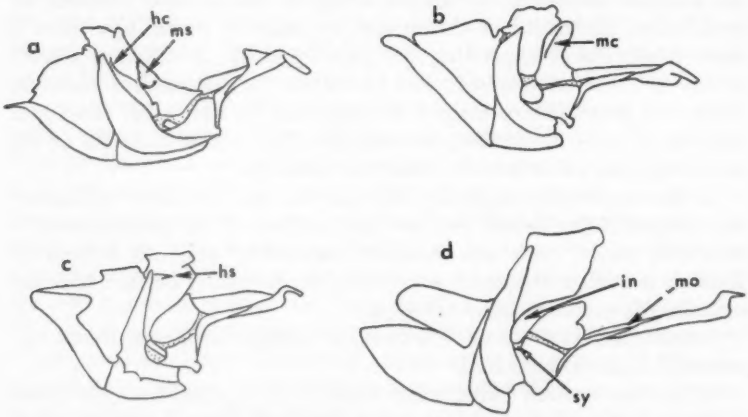

FIGURE 8.—Right suspensoria and opercular bones: *a, Prolatilus jugularis; b, Bathymaster signatus; c, Trachinus draco; d, Notogrаptus guttatus.* (hc=Hyomandibular crest, hs=hyomandibular spine, in=interspace between upper and lower portions of suspensorium, mc=metapterygoid crest, mo=mesopterygoid, ms=metapterygoid strut, sy=symplectic.)

The parapercid genus *Prolatilus* (fig. 8*a*) seems to be the only member of the Blennioidei to retain the rather typical percoid metapterygoid strut (Katayama, 1958).

Across the surface of the back of the suspensorium, various crests develop for muscular attachment. Among the parapercids, such a ridge runs anteroventrally across the hyomandibular. In zoarcids (fig. 8*b*), it is usually on the metapterygoid. In *Trachinus* and uranoscopids, the hyomandibular sends forward a hooklike process (fig. 8*c*).

Various members of the Blennioidei lose a firm attachment between the anterior and posterior portions of the suspensorium. Among such

fishes are the trichonotid *Crystallodytes*, notograptids (fig. 8*d*), congrogadids, and possibly the zoarceoid *Ptilichthys* (Makushok, 1958, p. 66, fig. 38b).

The mesopterygoid is developed variously. In *Trachinus*, it is broad and in *T. draco*, it bears teeth. Another family in which, so far as known, it is consistently broad is the Trichonotidae. On the other hand, the mesopterygoid appears to be narrow throughout the zoarceoids.

GILL ARCH SYSTEM.—The gill arch system of the Blennioidei is basically percoid, with the lower pharyngeals always separate. Only two modifications in the Blennioidei will be noted. The first, occurring in the congrogadoid *Notograptus*, is that the posterior basibranchials have dropped out. The second, which recurs repeatedly, is that the three upper pharyngeal tooth patches become reduced to two or, in blenniids, to one.

DORSAL PORTION OF THE HEAD (fig. 9).—The frontals usually are paired in the Blennioidei; however, in at least the tropical blenny *Runula*, the frontals of the two sides seem to have fused.

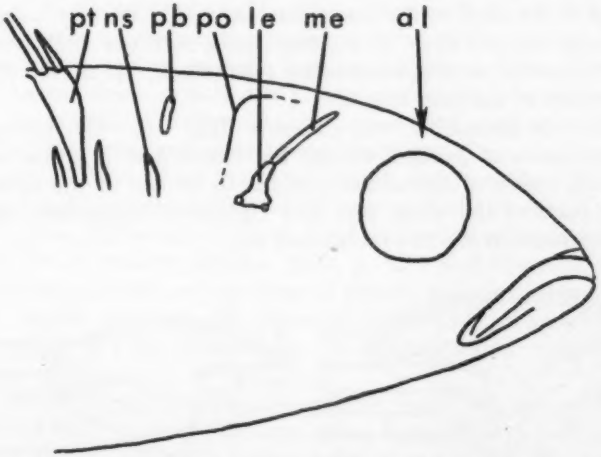

FIGURE 9.—Diagram of certain structures in *Prolatilus jugularis* (al = anterior level reached by the body musculature extending over the cranium, le = lateral extrascapular, ns = upper end of neural spine, pb = predorsal bone, po = posterior rim of supraoccipital, pt = pterygiophore of first two dorsal spines).

On the dorsal surface of the cranium posteriorly, the Blennioidei in general differ from the typical percoid in that the body musculature does not extend forward over the skull, and the supraoccipital and frontal-parietal crests, which, in part, form surfaces of attachment

for such musculature, usually are missing; however, in *Prolatilus* (fig. 9), a very generalized genus of the notothenioid family Parapercidae, the usual percoid condition is retained; furthermore, as in the percoids, the supratemporal commissure is incomplete, ending blindly over the musculature.

Generally, in the Blennioidei, the supratemporal commissure is complete. In such fishes as most notothenioids, all congrogadoids, trachinids, and certain tropical blennies of the families Tripterygiidae (Rosenblatt, 1957, unpubl. Ph.D. dissertation) and Clinidae, the supratemporal canal runs up on each side through the lateral and medial extrascapulars and then crosses the midline in a membranous tube; however, in the "uranoscopoid families," in most tropical blennies, and in all the zoarceoids, the medial extrascapular appears to have fused with the parietal.

Certain tropical blennies and zoarceoids have secondarily developed crests on the skull; e.g., a median crest along the frontals. Such crests, however, are for the attachment of jaw musculature, not body musculature (Makushok, 1958, p. 51).

Even though a supraoccipital crest rarely occurs on the dorsal surface of the skull in the Blennioidei, a small crest may be retained on the posterior surface. In the zoarceoids, with the single exception (known to me) of *Cryptacanthodes* (Makushok, 1961a, fig. 3), even this section of the crest is lost.

SPHENOID REGION OF THE CRANIUM (fig. 10).—So far as the differentiation of lineages among the Blennioidei is concerned, the sphenoid region of the cranium seems to be one of the most diagnostic parts of the whole fish. The features of importance here are the basisphenoid and the postorbital bar.

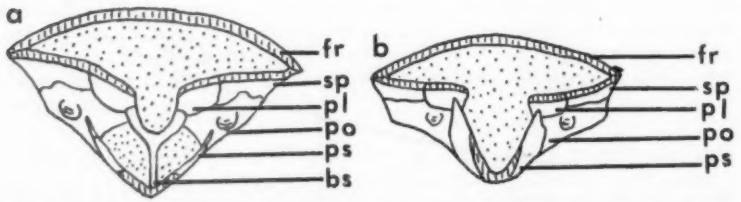

FIGURE 10.—Diagrammatic cross-section of cranium, looking toward rear, at level of front of basisphenoid: *a, Prolatilus jugularis; b, Bathymaster signatus.* (Vertical hatching=cut areas, stippling=cranial cavity, bs=basisphenoid, fr=frontal, pl=pleurosphenoid, po=prootic, ps=parasphenoid, sp=sphenotic.)

The basisphenoid is a bone that has been lost repeatedly in fishes. In general, this loss seems to be associated with the development of a broad, depressed cranium (see p. 21). Thus, among the noto-

thenioids, the basisphenoid, though generally present, is lacking in the flat-headed *Bembrops* and is said to be absent (Regan, 1913, p. 141) in the Hemerocoetidae. Among the tropical blennies and their relatives, it is apparently always present. In the zoarceoids, there is no basisphenoid.

In the zoarceoid *Bathymaster*, the brain cavity is separated from the posterior myodome only by membrane anteriorly (fig. 10*b*), though posteriorly there appears to be the usual horizontal prootic ledge separating the two cavities. In such a fish as the parapercid *Prolatilus* (fig. 10*a*), by contrast, the myodome is separated almost completely from the cranial cavity by the wings of the basisphenoid anteriorly and by a well-developed prootic ledge posteriorly. This is the usual percoid condition. (For an account of variations of the posterior myodome in scorpaeniform fishes, see Quast, 1965, pp. 574, 584.)

In the basal percoids, the ascending wing of the parasphenoid is low (as in fig. 4) and does not extend up to a junction with the pleurosphenoid in front of the prootic. But again and again in the percoid derivatives—and, for that matter, in lower teleosts (see, e.g., figs. in Svetovidov, 1948)—the ascending wing of the parasphenoid becomes prolonged upward in front of the prootic to the pleurosphenoid and, in extreme instances, meets a descending wing of the frontal ahead of both the prootic and pleurosphenoid. Starks (1923, pp. 261–263), Makushok (1958, pp. 41, 42), and Quast (1965, pp. 572–574) discuss variations in this character.

Among the Blennioidei, the parasphenoid always extends up to the pleurosphenoid or frontal ahead of the prootic in the Zoarceoidae and Trachinoidae; it does not do this in the Notothenioidae. In the tropical blennies, it is variable (Starks, 1923, p. 263, and Springer, 1966). Among congrogadoids, a long sliver of prootic extends forward to the orbital border between the pleurosphenoid and parasphenoid in *Congrogadus*, but in *Notograptus* the parasphenoid and pleurosphenoid meet.

FIN STRUCTURE.—With a few exceptions, the differentiation between spines and soft rays is not as clear in the Blennioidei as it is in most percoids. On the one hand, pungent spines and their large pterygiophores tend to be reduced or lost. The tropical blennies are the only group that consistently has dorsal fin spines. On the other hand, the branching of the soft rays usually is reduced; where it does occur in the vertical fins, the posterior half of each branch rebranches sooner than the anterior half. In many blenniid genera, e.g., *Medusablennius* (Springer, 1966), there are no branched fin rays at all.

PAIRED FINS AND THEIR GIRDLES.—As noted above, the function and structure of the paired fins in the Blennioidei are different from

what they are in the percoids. In the percoids, the pectorals may be used to govern the vertical plane of forward movement, for stopping, turning, "treading water," and even in some—e.g., the labrids—for forward locomotion. One of the structural features that permits all of these activities is the ability to rotate the pectoral base around the upper ray as an axis. In the percoids, the uppermost pectoral ray articulates with the scapula (as in fig. 11*a*), but the lower rays articulate with progressively longer and independently movable actinosts. (If the outer ends of these actonosts are swung outward and downward, the pectoral fin base is brought into a plane vertical to the water; if they are swung up and back, the fin base moves toward a horizontal plane.) Among all but the most generalized of the Blennioidei (fig. 11*a*), both the function and structure of the pectoral change considerably. These fins (except in tropical blennies), instead of being used in maneuvering, may act as props against the bottom and, by being brought back sharply against the body from a somewhat erect position, may provide a fast standing start from the normal stationary position. Structurally, the pectorals of the Blennioidei, except where secondarily reduced as in the Congrogadidae, almost always are rounded and broad based. The pectoral girdle tends to have broad actinosts rigidly attached to the scapula and coracoid and to one another in order to form a rather rigid, platelike surface of attachment for the pectoral rays. In one group of the Blennioidei, the Notothenioidae, the platelike nature of the primary girdle frequently has been increased further by the fusion of the uppermost actinost with the scapula, reducing the autogenous actinosts to three. This has occurred in the Bovictidae, Nototheniidae, Harpagiferidae, Bathydraconidae, Channichthyidae, and the trichonotid (sensu lato) *Hemerocoetes* (fig. 11*b*).

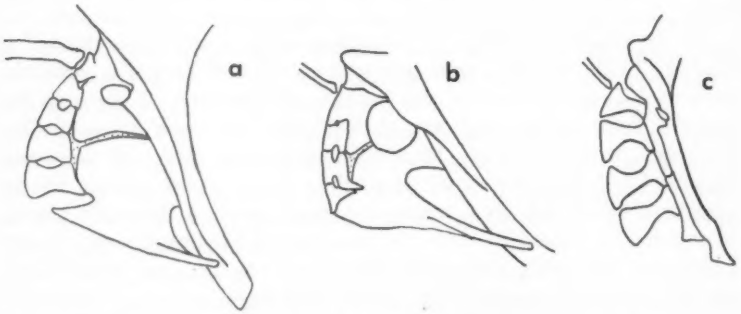

FIGURE 11.—Primary pectoral girdle, right side: *a*, *Prolatilus jugularis*; *b*, *Hemerocoetes* species; *c*, *Labrisomus nuchipinnis*. (In each figure, position of base of uppermost pectoral ray is shown.)

Regan (1913, p. 141) states that the trichonotid (sensu lato) *Bembrops* also has three actinosts, but I find four in two specimens identified as *B. gobioides*.

Inasmuch as the possibility for pectoral rotation has been largely lost in most of the Blennioidei, the differentiation between the uppermost ray articulation and that of the lower rays diminishes. Indeed, several of the upper pectoral rays usually move up to an articulation on the scapula along with the uppermost.

The tropical blennies, with the batrachoids and lophioids (Starks, 1930), are unique among teleosts in that they have developed secondarily an ability to rotate the fins—but not on the uppermost ray articulating with the scapula as an axis. Except in the Tripterygiidae, the pectoral rays all articulate with separately movable actinosts (fig. 11*c*). (The axis for maximum rotation for such a fin theoretically would lie between the two middle actinosts.)

The pelvic fins in the Blennioidei, when present, are always in advance of the pectoral bases, though in a few of the generalized forms, like the parapercid *Prolatilus*, not much so.

Among the Blennioidei, three things happen to the pelvic fins. One, which seems to have no phylogenetic significance, is that, in elongate fishes, the pelvics tend to dwindle in size and disappear completely. A sequence of this sort can be followed in the notothenioid family Trichonotidae (*Apocreedia*), in the congrogadoids, and in the zoarceoids (Makushok, 1958).

Those Blennioidei in which the pelvics are not minute or absent seem to have put them to two rather different uses. In one, represented by the Dactyloscopidae, almost all the Blennioidae, and to some extent the Trachinidae, the two or three outer soft rays are simple, somewhat strengthened, and recurved at their tips, which extend well beyond the membrane between them. Usually such fins are held more or less erect under the body.

In the other type of development, the pelvic fins are held back flat against the abdomen, but all five rays are retained, none are strengthened, and the inner are at least somewhat the longest. In this type of development, which occurs in almost all of the the Notothenioidae and in the Leptoscopidae, the pelvics frequently become separated widely from one another. Such fishes must rest with their thoracic areas between the pelvics in direct contact with the substrate.

The pelvic girdles of the Blennioidei are very varied. The only taxonomically meaningful structural peculiarity that I could find is that mentioned under the Trachinoidae (see p. 59).

VERTICAL FINS.—The basic dorsal fin arrangement that runs through many of the Blennioidei is a short, anterior spinous dorsal followed by a long, low fin of soft rays. Especially in the eel-shaped forms,

the separate anterior spinous dorsal is lost, and there is a single long dorsal fin that may be made up entirely of soft rays (*Congrogadus*), almost entirely of spines (*Notograptus*), or partly of each (Blenniidae). The anteriormost dorsal ray is almost always far forward, and generally there are no predorsal bones (Smith and Bailey, 1961); however, the notothenioid genus *Cheimarrichthys* does have the basal percoid number of three predorsals, and *Congrogadus* has two.

The anal fin of the Blennioidei rarely contains pungent spines (see, however, Makushok, 1958, p. 34), though one or two unsegmented anterior rays frequently are present. Among the percoids there is usually a more or less constant relationship between the anterior anal pterygiophores and the first hemal spine. Among percoids with large, pungent anal spines, the two or three first anal pterygiophores frequently are fused; however, in forms with smaller anal spines, such as *Acanthoclinus* or the opistognathid *Gnathypops*, they remain separate. In *Acanthoclinus*, the first anal pterygiophore extends up behind the first hemal spine; in *Gnathypops*, the first pterygiophore is short, and the second extends up behind the anteriormost hemal spine. This more or less constant relationship between the anterior anal pterygiophores and the first hemal spine is maintained in the members of the family Tripterygiidae, Clinidae, and Blenniidae that I have examined; however, it is lost in the other groups of Blennioidei. Most frequently, e.g., in the Parapercidae, Trachinidae, and Bathymasteridae, the first few anal pterygiophores are short and well forward of the first hemal spine. The great variation that may occur even within a group has been demonstrated by Makushok (1958, p. 29) for zoarceoid families.

Posteriorly, the dorsal and anal usually approach and sometimes are connected membranously with the caudal fin. Only in some of the clinine clinids is there a lengthy, constricted caudal peduncle behind the dorsal and anal. Where it does occur, it is supported, as elsewhere, by expanded, bladelike neural and hemal arches—e.g., among the ammodytoids (Gosline, 1963).

CAUDAL FIN AND CAUDAL SKELETON.—In the Blennioidei, the fin is generally rounded or it is brushlike. Exceptions may be divided into two categories. One contains certain of the secondarily pelagic forms that have a somewhat lunate caudal fin, e.g., the tropical blenny *Runula*. The other is made up of certain basal notothenioids with bilobed tails. Certain species of *Parapercis* (Cantwell, 1964) and possibly *Cheimarrichthys* fall into this category.

As so often happens among fishes with rounded caudal fins, the number of branched rays becomes variable (Makushok, 1958). In the Blennioidei, the notothenioid Parapercidae is the only family that

maintains the usual percoid number of 15 branched rays, all other families having a reduced number.

In the caudal skeleton, the amount of fusion and/or loss varies all the way from an almost basal percoid condition (Gosline, 1961b) to a single bone (Makushok, 1958). The whole gamut is covered in the notothenioid group and to a lesser extent in the others. At the very base is *Parapercis* (Gosline, 1963, p. 95, fig. 6) with five hypurals (counting as in Nybelin's 1963 system), one uroneural, three epurals, and three hemal arches—all of these elements autogenous, i.e., separate. In *Trachinus* (fig. 5*b*), at the base of the trachinoid-blennioid-congrogadoid series, there are only 11 branched rays in the caudal fin, and the two hypurals to the lower portion of the caudal fin have become fused, but the other elements are as in *Parapercis*. In *Bathymaster*, at the base of the zoarceoids, there are 14 branched rays; the last hemal arch has fused to the lower hypurals to form a single element supporting the bottom half of the caudal fin, but there are still three separate upper hypurals, a uroneural, and three separate epurals (fig. 5*c*). All of the above fishes show less fusion in the caudal skeleton than such percoids as *Acanthoclinus* and *Opistognathus*.

The pathways of fusion seem to be about the same in the various groups of Blennioidei. Thus, a general first stage seems to be a fusion of the lower hypurals (*Trachinus*, fig. 5*b*) followed by an ankylosis of these with the last hemal arch (*Bathymaster*, fig. 5*c*). This single element fused to the lower part of the caudal fin remains separate from the last centrum until after all of the upper hypurals and the uroneural have fused to the urostyle.

VERTEBRAL COLUMN AND RIBS.—The basal percoids tend to have a rather standardized vertebral column with 24 or 25 vertebrae, 10 abdominal and 14 or 15 caudal. This basal number always is exceeded among the Blennioidei. The increase in the vertebral number occurs first in the caudal section of the column; in the abdominal section, members of the Parapercidae (Cantwell, 1964), Tripterygiidae (Gosline, 1963), and Leptoscopidae (Regan, 1913) all are recorded with 10 abdominal vertebrae.

Ribs may be quite variable among the Blennioidei. Among the flatter forms, pleural ribs may be lacking completely, as in *Bembrops* and the leptoscopids. Pleural ribs also are lacking in the elongate Pholidae (Makushok, 1958, p. 28). In the Uranoscopidae, pleural and epipleural ribs both are attached to independent bony struts that Starks (1923, p. 279) has called basipleurals. More frequently, however, the usual percoid configuration of epipleural ribs from the first, pleural ribs from the third vetebra, is present. From structure, it is sometimes difficult (e.g., among congrogadoids) to distinguish pleural from epipleural elements.

Relationships of the Blennioidei

In the first part of this section, the Blennioidei have been delimited. Within the group, there is a whole series of what might be called central tendencies that will distinguish the group from its ancestral percoid type. Thus, in the Blennioidei, the body musculature (except *Prolatilus*) does not extend forward over the top of the head, and supraoccipital and frontal-parietal crests for its attachment are lacking. The supratemporal commissure usually is complete, extending across the supraoccipital. There are always more than 25 vertebrae. Predorsal bones usually are absent. The anal fin rarely has pungent spines, though there may be one of two unsegmented rays anteriorly; the anterior interhemals are not enlarged and do not abut against the first hemal arch. The pelvic fins either have fewer than five soft rays or the inner rays are the longer. Pectoral and caudal fins usually are rounded. In the caudal (except Parapercidae), there are fewer than 15 branched rays. The gas bladder usually is absent in the adult.

Most or all of the above characters are associated with the basal mode of life of the Blennioidei noted previously; however, some members show secondary modifications. These cause some of the principal difficulties in distinguishing the lineages within the suborder (fig. 12) and, for that matter, in defining the Blennioidei. Thus, certain members of the Blennioidei of various ancestries have developed secondarily a more or less pelagic existence, e.g., the petroscirtines among tropical blennies and *Zaprora* among zoarceoids. When this happens, the tail may be more or less lunate, as in *Runula*, instead of having the rounded form typical of the Blennioidei. Furthermore, the pelvic rays of the petroscirtines tend to become filiform and weak (completely lacking in *Plagiotremus*) rather than sturdy, as in other tropical blennies.

Some forms of the Notothenioidae and Blennioidae and all of the Trachinoidae apparently bury themselves at least up to the eyes in sand. This obviously creates several problems in breathing and probably is associated with the wide gill openings of the notothenioid family Trichonotidae and the superfamily Trachinoidae (see previous section), as contrasted with the usual ventral restriction of the gill slits in the Blennioidei.

Certain members of the notothenioid family Trichonotidae have become sand divers. Here, as elsewhere when this habit occurs—e.g., in the Ammodytidae and Kraemeriidae—certain morphological features seem to develop. Thus, unlike the rest of the notothenioids, the pelvics of sand-diving trichonotids are close together and may be reduced or disappear completely, as in, e.g., *Apocreedia*.

Among eel-shaped forms, there is the usual tendency for the pelvics to dwindle away and disappear first, followed by the pectorals. These

FIGURE 12.—Diagram of blennioid relationships (groups above diagonal double line have exact 1:1 ratio between dorsal and anal rays and vertebrae; groups below double line have slightly more than 1 fin ray per vertebra).

trends are encountered not only in the more elongate zoarceoids, but also in the congrogadoids.

In regard to what would seem to be primary phylogenetic differences (fig. 12), the Blennioidei appear to be divisible into three main groups: a notothenioid, a zoarceoid, and a trachinoid-blennioid-congrogadoid series. These three groups (see fig. 12) are contrasted in table 2.

In many respects, evolution within the three groups has progressed along parallel lines; for example, in the progressive fusion of elements of the caudal skeleton. On the other hand, the same trend of development may occur in all three, but apparently has progressed at different rates. Thus, among the notothenioids, the medial extrascapular remains free of the parietal in all of the forms I have examined except *Harpagifer;* in the trachinoid-blennioid-congrogadoid series, it frequently fuses with the parietal; and in the zoarceoids there is no trace of a free medial extrascapular. Finally, there are indications of secondary convergence of characters in the three series, as among the pelagic and the burrowing forms already noted.

But for all these difficulties, the three do show certain primary differences in evolutionary development. Thus, the notothenioids have tended to flatten the head and anterior portion of the body. Probably associated with this are peculiarities of paired fin structure. With the exception of certain sand-diving trichonotids, the pelvics are well separated and maintain a full complement of five soft rays, with the inner usually the longest; these pelvics normally are held back flat against the body. In the pectoral girdle, the actinosts are always broad and platelike, and the uppermost frequently fuses with the scapula. In the above features, the notothenioids have developed along lines that are not duplicated elsewhere in the Blennioidei. Conversely, the notothenioids retain certain percoid features that most of the other members have lost. Of these, the independent medial extrascapular already has been mentioned. More important, the parasphenoid in notothenioids (fig. 10*a*) has no wing extending in front of the prootic in such a way as to exclude the prootic from the internal orbital border.

The notothenioids have, morphologically speaking, the longest lineage in the Blennioidei. They extend from the Parapercidae, the most percoid-like family of the Blennioidei, out to the Callionymidae and Gobiesocidae. The latter groups show quite clearly all the trends of notothenioid development listed above (except that the Gobiesocida have only four pelvic rays), and the specializations that seem to warrant their exclusion from the Perciformes altogether lie along other lines.

The other two main series of the Blennioidei rarely are flattened anteriorly, generally tend (for very different reasons) to reduce the number of pelvic rays, and, with the exception of the Leptoscopidae, never have the pelvics widely separated.

Of these two series, the Zoarceoidae, so far as known (but see below), are structurally the most homogeneous. There is among the zoarceoids a general trend toward elongation, and concurrently (as noted) for the pelvic fins, followed by the pectorals, to diminish and disappear. In skull characters, the zoarceoids are all specialized: there is no separate, medial extrascapular; the prootic always is excluded from the orbital border by the parasphenoid (fig. 10*b*); and there is no basisphenoid. In this last feature, the zoarceoids differ from all but a few of the other Blennioidei. The single nostril on each side of the head will distinguish immediately the zoarceoids from all tropical Blennioidei.

The trachinoid-blennioid-congrogadoid series is internally diverse. It is defined more easily in terms of lack of peculiarities that the notothenioid and zoarceoid lines have developed than in terms of its own specializations; nevertheless, there are two weak trends of development that may be noted for the trachinoid-blennioid-congrogadoid series. The first trend is toward a consolidation of the bones of the circumorbital ring. *Trachinus* (fig. 7*c*) and the congrogadoids are the only members of the Blennioidei with a well developed percoid-type subocular shelf, and from here there is usually a further fusion of circumorbital elements, rather than a disintegration of the circumorbital ring that tends to occur in the zoarceoids and notothenioids. This differentiation in circumorbitals, however, is not constant (see above). The second trend seems to be a tendency in the Trachinidae, Uranoscopidae, Dactyloscopidae, and tropical blennies to erect the close-set pelvics and use them as props under the body. This trend, however, does not extend to the Leptoscopidae, Congrogadidae, and Notograptidae.

If the specializations held in common by the trachinoid-blennioid-congrogadoid series are unimpressive, those that differentiate the three components of the series are well marked. In the first place, the three groups making up the series appear to have very different modes of life. The trachinoids, made up of the Trachinidae, Uranoscopidae, Leptoscopidae, and Dactyloscopidae, partially bury themselves in sand or mud (Gill, 1907) and apparently wait for or positively attract passing prey. Of the various morphological characteristics related to this habit, only one associated with respiration need be noted here. The gill covers extend down over the branchiostegal membranes, which are completely free from each other and from the isthmus (see p. 43). In the tropical blennies and congrogadoids, by

contrast, the gill covers are more or less broadly attached to one another or to the isthmus or both, and a different method of respiration must be used.

The tropical blennies (Blennioidae), though some members secondarily have taken up a different mode of life, are fishes that basically prop themselves off a hard bottom by means of one or more strengthened pelvic rays. Though the number of pelvic rays always is reduced from the five usually found in the trachinids and others, the pelvics, except in secondarily pelagic forms, are never rudimentary as they are in the congrogadoid group. Another feature found in all but the most generalized tropical blennies, i.e., the Tripterygiidae, is that the uppermost pectoral ray articulates with an actinost rather than the scapula. In this character, unique, to my knowledge, among the Blennioidei, the tropical blennies approach the batrachoid fishes (Starks, 1930). Also, the Blennioidae are the only superfamily in the suborder in which a large anterior portion of the dorsal fin (or fins) is made up usually of spines.

The congrogadids, with their allies the notograptids and possibly the peronedyids, are enigmatic eel-like forms. In these, the front and back of the suspensorium are associated loosely. They hold with the Trachinidae, alone among the Blennioidei, a subocular shelf, but this is a trait inherited from the percoids.

An attempt to establish the most generalized, i.e., percoid-like, families among the Blennioidei leads down to the Parapercidae (notothenioids), on the one hand, and the Trachinidae (trachinoid-blennioid-congrogadoid series), on the other (fig. 12). Yet the percoid characteristics that these two families retain are rather different. In the parapercid genus *Prolatilus*, there is a percoid supraoccipital crest and incomplete supratemporal commissure, no strut from the parasphenoid extending up in front of the prootic, 10 abdominal vertebrae in *Parapercis*, five separate hypurals (counting as in Nybelin's 1963 system), and 15 branched caudal rays. The generalized features of *Trachinus*, on the other hand, are the broad subocular shelf and the toothed mesopterygoid of *T. draco*. Though the parapercids and trachinids already have evolved in somewhat different directions, a basal percoid family such as the Branchiostegidae could, so far as morphology is concerned, stand at the base of both. Indeed, the superficial similarities are such that it is sometimes difficult to separate the members of the Branchiostegidae from the Parapercidae (however, see p. 43). As for the trachinids, it is not necessary to go so deeply into the percoid stock to find a fish that would provide a morphologically ancestral type. Except for certain specializations, e.g., fusion of elements in the caudal skeleton, *Opistognathus* or *Acanthoclinus* seem to serve fairly well. These genera already have the

erectile pelvic fins well ahead of the pectorals and other typical (if not universal) trachinoid features; however, as already suggested, there is no morphological reason why the opistognathids and acanthoclinids, as well as the trachinoids, should not have been derived from some basal percoid near the Branchiostegidae.

In the section that follows, the Blennioidei, essentially the Jugulares of Jordan (1923), will be considered a suborder of the Perciformes. The reasons for this are as follows: First, the members of the Blennioidei form a recognizable, definable group of fishes. Second, though I am as dubious about a strictly monophyletic origin for the Blennioidei (within the limits of that suborder as herein defined) as those who have investigated the group before me—e.g., Regan (1913, p. 138) and Starks (1923, p. 264, ftn. 1)—it seems possible that the ancestors of the various groups of Blennioidei lie deep in the basal percoids not too distant from one another. Finally, those who insist on strictly monophyletic groups would be forced, I think, into the alternative of recognizing at least three and probably five separate suborders among the Blennioidei. This possibility has been considered and rejected.

Classification of the Blennioidei

In the present section, for the sake of completeness, the classification of the suborder Blennioidei (=order Jugulares of Jordan, 1923 in part) is carried down to family. For the contents and a definition of this suborder as understood here, see p. 40.

SUPERFAMILY NOTOTHENIOIDAE (= Superfamily Notothenioidae+ Trachinoidae, in part, of Berg, Regan, and Norman).—Head and anterior part of body usually more or less flattened. One nostril on each side in the nototheniid fishes (sensu lato), two on each side in the rest. Gill openings extending far forward in the Bovictidae and Trichonotidae (sensu lato), the gill membranes attached to one another or broadly attached to the isthmus in the rest. Branchiostegal rays seven in the Bovictidae and most Trichonotidae (sensu lato), six in the rest. Circumorbital series of bones usually movably connected, sometimes incomplete, without a subocular shelf on the second. Front and rear portions of suspensorium firmly attached except in some Trichonotidae (sensu lato). Prootic forming a part of the internal orbital border. Basiphenoid usually present.

Pectoral actinosts platelike, three or four in number, the upper pectoral ray or rays articulating with the scapula. Pelvic fins, except in some Trichonotidae (sensu lato), with a spine and five branched soft rays, the interspace between pectoral bases usually broader than the distance across one pelvic base.

The Notothenioidae are the only superfamily of the Blennioidei represented in both tropical and cold waters. Around the Antarctic

continent, this is the dominant group of fishes. The Notothenioidae also are the only superfamily to contain freshwater members (*Cheimarrichthys* and *Pseudaphritis*).

Aside from the Gobiesocidae, Draconettidae, and Callionymidae, which herein are removed from the Perciformes entirely, the members of the notothenioid lineage (fig. 12) seem to fall into three or four groups:

At the base of the whole lineage are the two families Parapercidae and Cheimarrichthyidae. These retain predorsal bones and a number of other percoid features that have been lost by the rest of the notothenioids and, for that matter, the other members of the Blennioidei. (*Cheimarrichthys* does not, however, have an orbitosphenoid as stated by Lane, 1965).

A second group is made up of the notothenioids (sensu stricto), namely the Bovictidae, Nototheniidae, Harpagiferidae, Bathydraconidae, and Channichthyidae (Norman, 1957). This group is characterized by the three pectoral actinosts, by a single nostril on each side of the head, and by its primarily Antarctic distribution; however, the distinction between this and other groups is not as clear-cut as it appears from the literature. The presence of only three actinosts occurs in the notothenioid (sensu lato) derivative Callionymidae and in the "trichonotid" *Hemerocoetes*, which, with other "trichonotids," has two nostrils on each side of the head, although the first may be very small; but the derivative Callionymidae and also *Melanostigma* (see under Zoarceoidae) have only one.

The third group is made up of the Trichonotidae (sensu lato) (Schultz, 1960, pp. 273–277; except *Cheimarrichthys*, among the genera I have seen). This group contains a wide spectrum of morphological variation; however, the members I have been able to examine have the following features in common: The gill openings extend far forward under the throat, as in the Bovictidae among notothenioid (sensu stricto) families. The branchiostegal rays are seven, except *Hemerocoetes*, which has six. The ascending process of the premaxillary is attached movably to the toothed portion. At least in *Crystallodytes*, *Bembrops*, and *Hemerocoetes*, the mesopterygoid forms a broad shelf, free posteriorly, but attached to the palatine anteriorly; the palatine, in turn, is attached movably to the pterygoid. Though these characters are quite distinctive, *Hemerocoetes* with three actinosts may be intermediate between the Trichonotidae and the Bovictidae among notothenioid families.

A possible fourth group is represented by *Melanostigma*, which (see p. 63) may prove to be merely a pelagic notothenioid (sensu stricto).

SUPERFAMILY TRACHINOIDAE (=Trachinidae, Uranoscopidae, Leptoscopidae and Dactyloscopidae).—Head compressed or rounded. Two external nostrils on each side. Gill openings extending far forward. Circumorbital bones firmly connected, more or less expanded onto the cheek, sometimes with a subocular shelf on the second. Medial tabular firmly attached, but not fused to parietal. Front and rear of the suspensorium firmly connected. Prootic not forming a part of the internal border of the orbit. Basisphenoid present.

Pectoral actinosts four, broad or columnar, the upper pectoral ray articulating with the scapula. Pelvic fins with a spine and five soft rays (except Dactyloscopidae), the interspace between them less than the distance across one pelvic base (except Leptoscopidae).

The trachinoids possess two additional characters in which, to my knowledge, they are unique among the suborder Blennioidei. In the pelvic girdle, the ridge on which the pelvic spine rides extends forward into a point. This point may lie adjacent to its fellow on the opposite side of the midline, as in *Trachinus*, *Leptoscopus*, and *Dactyloscopus*, or form a more laterally located projection from the flesh, as in the Uranoscopidae. The second peculiarity is that at least *Trachinus* and *Uranoscopus* have a bony point extending forward from the outer surface of the posterior rim of the hyomandibular (fig. 8*c*). Further similarities are as follows: In all four families, the scapular foramen is very large and, except in the Leptoscopidae (Starks, 1930, p. 226), extends to the cleithrum. All four families have a low number of abdominal vertebrae (10–12) for the Blennioidei. Certain other tendencies among the trachinoids may be associated with their habit of living in the sand or mud. One is the development, in some trachinids and uranoscopids, of a continuity between adjacent scale edges to form ridges extending down and back across the body. Another is for the mouth to have a fringed border. Finally, the circumorbital bones are more or less expanded down over the cheek; armature is usually developed; and the top of the head is frequently rugose.

The Trachinoidae is made up of tropical and temperate marine fishes occurring on soft bottoms in which they bury themselves up to the eyes (Gill, 1907).

On the basis of the reduction in pelvic ray number in the Dactyloscopidae, Regan (1912d) placed this family in a different suborder from the Uranoscopidae and Leptoscopidae. Starks (1923) pointed out the artificiality of this procedure. On the other hand, Starks denied any relationship between the Trachinidae and the "uranoscopoid" families. To me, the evidence to the contrary given above seems wholly convincing.

SUPERFAMILY CONGROGADOIDAE (=Congrogadidae, Notograptidae, and provisionally the Peronedyidae).—Head compressed or rounded.

Two nostrils on each side. Gill openings somewhat restricted below. Circumorbital series of bones firmly connected, complete, with a subocular shelf from the second. Medial extrascapular not fused to the parietal. Front and rear of the suspensorium loosely connected. Prootic forming a part of the internal orbital border or not. Basisphenoid present.

Pectoral actinosts columnar, four in number, the upper pectoral ray articulating with the scapula. Pelvic fins minute or absent; if present, the interspace between them less than the distance across one pelvic base.

The suborder is entirely inshore, tropical Indo-West Pacific in distribution.

The families included here in the Congrogadoidae are the Congrogadidae, Notograptidae, and very provisionally the Peronedyidae. In 1952 Smith divided the Congrogadidae of Regan (1912d) into two families, the Congrogadidae and Haliophidae. This seems, however, an unnecessary proliferation of families among obviously related fishes. Besides, the type of *Congrogadus heirichthys* and, for that matter, juveniles of *C. subducens* fall between the two families as Smith defines them.

So far as the congrogadids and notograptids are concerned, a relationship between the two families needs demonstration. This is by no means easy, despite the general eel-like form in both; however, both have a subocular shelf on the second suborbital bone, a feature held in common with *Trachinus* and many percoids. Second, though the mechanism is different in the two families, both have a suspensorium in which the anterior half is connected only weakly with the posterior portion. Third, the soft dorsal and anal rays show a type of branching that does not extend to the base but in which the posterior, but not the anterior branch, redivides. (The Peronedyidae are based on a single Australian species I have not seen, the affinities of which are doubtful. It will not be discussed here.)

Granting a relationship between notograptids and congrogadids, the question then arises as to what the two families are in turn related to. Smith (1952, p. 87) suggests that the congrogadids may be aberrant percoids. This is a distinct possibility, but Smith's further suggestion of "Spariform relations" seems most improbable. The anterior pelvic position of *Notograptus* and certain congrogadid genera and the 1:1 relationship between dorsal and anal rays and vertebrae suggest the Blennioidei, and there seems to be no reason to deny them such an allocation.

An effort to locate possible relatives of the Congrogadoidae has led to an investigation of certain other eel-shaped fishes. The results, though negative, may be noted briefly.

In *Mastacembelus liberiensis* (USNM 118751), there are no pelvic fins. The dorsal and anal rays are somewhat more numerous than the vertebrae. The structure of the trunklike snout seems to be unique in fishes. The nasal bone (Regan, 1912a, fig.) forms a long lid over the nasal cavity. It is attached tightly by ligament to the ethmoid medially and along its outer surface to the lacrimal. In the cavity below the nasal bone, there is a long nasal organ of the same gross shape as that of *Anguilla;* however, the nasal organ of *Mastacembelus* is folded over on itself with the fold hinge medial. The nasal epithelium extends down from the top fold and up from the bottom one as a series of transverse leaves, and the water apparently passes between the two folds. The posterior nostril is just ahead of the eye, but the anterior is at the end of a tube at the front of the trunk. Just above the anterior nostril on each side is the opening to another long, membranous tube that connects posteriorly with the supraorbital sensory canal at the front of the nasal bone. The upper jaw is suspended far forward, below the rostral "trunk," from a membranous extension of the mesethmoid. The maxillary has no connection whatsoever with the palatines, and neither the premaxillary nor the maxillary have the usual articular surfaces or pedicels.

A fish that possibly is related more closely to the Congrogadoidae than *Mastacembelus* is *Alabes.* In *Alabes,* the premaxillary pedicels extend up under the nasal bones, as in *Congrogadus,* and the anterior and posterior portions of the suspensorium are disconnected. *Alabes,* however, is so specialized (degenerate) as to have obscured any real evidence of relationship; *Alabes* has no supratemporal canal, no dorsal or anal fin rays, and no primary pectoral girdle. Under the circumstances, it seems best to leave *Alabes,* at least provisionally, in the Symbranchiformes, where it usually is placed (Regan, 1912c).

Superfamily Blennioidae (= Tripterygiidae, Clinidae, Chaenopsidae and Blenniidae).—Head compressed or rounded. Two nostrils on each side. Gill openings more or less restricted below, the gill membranes attached to one another or to the isthmus. Circumorbital bones usually firmly connected, without a subocular shelf from the second. Medial tabular usually fused to the parietal. Front and rear of suspensorium firmly connected. Prootic usually excluded from the internal orbital border. Basisphenoid present.

Pectoral actinosts columnar, longer than the scapula and coracoid are broad (fig. 11*c*), the upper pectoral ray articulating with an actinost (except Tripterygiidae). Pelvic fins with two to four soft rays of which the outer are strengthened and the membrane between the rays deeply incised (except such secondarily pelagic forms as *Aspidontus, Runula, Xiphasia*). Dorsal and anal soft rays usually unbranched.

An additional feature that seems to separate the Blennioidae from all other members of the suborder is that the members I have examined, at least, retain a constant relationship between the anteriormost anal pterygiophores and the first hemal spine.

Members of this superfamily are abundant inhabitants of all tropical inshore areas, and some extend their ranges well into temperate waters.

The relationship of the tropical blennies to any other fish group is by no means clear.

SUPERFAMILY ZOARCEOIDAE (=Zoarceoidae+Stichaeoidae+Cryptacanthodidae of Makushok+Bathymasteridae+Zaproridae+?Derepodichthyidae+?Scytalinidae).—As Norman (1957, p. 477) indicates, *Zoarcaeus* Nilsson, 1832, appears to be the first Latinized version of Cuvier's (1829, p. 400) "Les Zoarcés." But *Zoarcaeus* is an objective synonym of *Enchelyopus* Gronow, an invalid name that, depending upon interpretation, may have been validated nomenclatorially by Scopoli (1777). Though the proper generic name to be used herein is by no means clear, the family group names Zoarceoidae and Zoarcidae are available whether or not the generic name on which they are based is a synonym ("International Code of Zoological Nomenclature," 1964, p. 11).

Head compressed or rounded. The body is long and more or less tapering posteriorly, with a short, usually poorly demarcated caudal peduncle. A single nostril on each side of head. Gill openings rarely (*Derepodichthys*) extending far forward below the head. Medial extrascapular of the usually well developed lateral line (seismosensory of Makushok) system fused to the parietals. Front and rear of the suspensorium usually firmly connected (apparently weakly connected in *Ptilichthys;* see Makushok 1958, p. 66, fig. 38b). Prootic excluded from the interior orbital rim. Basisphenoid absent.

Pectoral actinosts broad, usually four in number (said to be three sometimes in *Cebedichthys* [Starks, 1930, p. 83] and altogether absent in *Azygopsis* [Makushok, 1958, p. 106, fig. 72]), the uppermost pectoral ray articulating with the scapula. Pelvic fins with fewer than five soft rays (except Bathymasteridae), frequenlly absent; if present, none of the soft pelvic rays are strengthened or the interradial membranes between them deeply incised. Interspace between pelvic fins less than the distance across one pelvic base.

In addition to the above features, there are others common to most or all zoarceoids that will separate them from many of the other Blennioidei. First, the maxillary is much longer than the premaxillary, sometimes more than twice as long in such extreme instances as *Anarrhichas*. Second, the dorsal fin is always continuous (except for *Ptilichthys*, which has separate spines anteriorly). Third, the entop-

terygoid is never, to my knowledge, more than a narrow strut, and the metapterygoid frequently has a vertical crest along the posterior border of its outer face (fig. 8*b*).

The zoarceoids are one of the major marine, cold-water groups. They are found in both hemispheres but are primarily and basically northern. In depth, they range from the intertidal region to the deep sea. They are generally demersal but at least *Zaprora* and *Lycodapus* have developed secondarily a pelagic habit. *"Zoarces" viviparus* is unusual in being a viviparous form that frequently occurs in water of reduced salinity (Schmidt, 1917).

The foregoing account has been based largely on inshore forms that are more readily available and that have been investigated much more thoroughly (e.g., Makushok, 1958, 1961a, 1961b). These give an impression of homogeneity that may be belied when the more peculiar of the deep-water and pelagic "zoarceoids" have been studied more intensively. Of those that have been reported on, *Zaprora* (Chapman and Townsend, 1938) is, as McAllister and Krejsa (1961) pointed out, a not too abnormal stichaeid-like form; however, the so-called zoarcid *Melanostigma*, judging from Yarberry's (1965) description, gives every indication of being a modified notothenioid and not a zoarceoid at all. Thus, a basisphenoid, unknown in zoarceoids, is present in *Melanostigma*. Its parasphenoid wings are low and do not extend up to the pleurosphenoids in front of the prootic (Yarberry, 1965, p. 445, fig. 2). There are only three pectoral actionosts. Finally, *Melanostigma* has seven branchiostegal rays, a number found throughout the Bovictidae and in most of the Trichonotidae, but only among the Anarhichadidae of the zoarceoids (see p. 44).

Even the inshore zoarceoids, however, despite their morphological homogeneity and peculiarity, have caused what would seem to be an unnecessary amount of taxonomic confusion. Regan (1912d, 1913), for example, placed the Bathymasteridae in the suborder Percoidei and then mixed the remaining zoarceoid families in with the tropical blennies. Hubbs (1952) and Makushok (1958) rectified the latter error. As already noted, the two groups differ significantly in skull (see fig. 10) and fin structure and even in the number of nostrils.

The Bathymasteridae seem to be a perfectly good zoarceoid family in both skeleton and soft anatomy. In two features it stands on the percoid side of the Zoarceoidae and, hence, may be considered the most generalized family in the group. First, the pelvic fin contains a spine and five soft rays; in all other zoarceoids, the pelvic fin is reduced. Second, the ramus lateralis accessorius (Freihofer, 1963, p. 136) has a percoid-type pattern, rather than one which is of the ophidiid-brotulid type (in Zoarcidae), or reduced (in Pholidae or Stichaeidae). Rosen (*in* Greenwood, et al., 1966, pp. 389, 397), primarily on the

basis of Freihofer's data, has assigned the Zoarcidae to the order Gadiformes of the superorder Paracanthopterygii. Since, however, in other respects the Zoarcidae are very similar to the Bathymasteridae, with a typical percoid accessorius nerve pattern, I prefer to view the peculiar accessorius configuration in the Zoarcidae as a specialization within that group (as in the Brotulidae and Ophidiidae; see p. 24) rather than as an indication of relationship with the codfishes.

Table 3 will serve as a summary of the classification of the suborder Blennioidei adopted here.

Summary

The higher classification of the Order Perciformes adopted here can be summarized in synoptic form as follows.

To attempt a definition of this order that would exclude the Beryciformes and Zeiformes on the one hand and the various orders presumably derived from the Perciformes on the other is almost impossible (see Norman, 1957, pp. 58, 59); in any event, it would require more detail than seems warranted here.

SUBORDER PERCOIDEI.—(For reasons dealt with at the beginning of this paper, the Percoidei can be defined only in terms of central perciform tendencies, or negatively by lacking the combination of peculiarities that characterize the other perciform suborders.) Pelvic bones extending between and attached by a direct articulation to the cleithra; pelvic fins usually inserted about below the pectoral bases, normally with a spine and five, but sometimes fewer, soft rays, rarely altogether absent; dorsal and anal soft rays generally somewhat more numerous than the vertebrae between them. Basal counts in the Percoidei (and Perciformes) are as follows: vertebrae 24 or 25, frequently more, rarely fewer; anal spines three, predorsal bones three, and branched caudal rays 15, all frequently fewer, rarely more; and branchiostegal rays six, ranging from four to nine. (Compiled.)

Superfamilies (mainly following Regan, 1913, and Norman, 1957, but modified from the preceding account): Percoidae, Cirrhitoidae, Embiotocoidae, Pomacentroidae, Labroidae, Trichodontoidae, Ammodytoidae, Champsodontoidae, and Chiasmodontoidae.

SUBORDER MUGILOIDEI.—Pelvic bones without a cleithral articulation. (1) The pectoral fins are divided into two separate parts (Polynemoidar); or (2) the pelvic fins have been modified into a specialized clasping organ in the males (Phallostethoidae); or (3) the spinous dorsal is represented by a short fin well separated from the soft portion. (Compiled.)

Superfamilies (following Myers, 1935): Polynemoidae, Mugiloidae, and Phallostethoidae.

SUBORDER ANABANTOIDEI.—An epibranchial air-breathing organ; gas bladder extending posteriorly well beyond the body cavity; teeth usually present on the parasphenoid. (Compiled.)

Superfamilies: Anabantoidae, Ophicephaloidae, and Luciocephaloidae.

SUBORDER KURTOIDEI.—Ribs much expanded, enclosing the anterior portion of the gas bladder partially, the posterior portion completely; males with an occipital hook, formed by the supraoccipital, used for carrying eggs. (From de Beaufort and Chapman, 1951.)

This suborder contains the single genus *Kurtus*.

SUBORDER ACANTHUROIDEI.—High-headed, compressed fishes with more or less lunate caudal fins, the gill openings restricted below, and small mouths; nasal bones elongate, more or less rigidly attached to the cranium; teeth specialized, setiform in the Zanclidae, bicuspid to multicuspid in the rest; cleithra expanded below; additional armature present in the form of (1) a spine at the corner of the mouth in juvenile zanclids, (2) one or more spines on the caudal peduncle of acanthurids, or (3) a second pelvic spine in teuthids. (Compiled.)

Superfamilies: Acanthuroidae and Teuthidoidae (=Siganoidae).

SUBORDER OPHIDIOIDEI.—Pelvics, when present, consisting of one or two filamentous rays inserted ahead of the pectoral fins; dorsal and anal fins long and low, spineless except in *Gadopsis*, the rays considerably more numerous than the vertebrae between them; one or more of the first few ribs usually expanded. (Reworded from preceding account.)

The Ophidioidei generally have not been divided into separate superfamilies.

SUBORDER STROMATEOIDEI.—"Perciform fishes with toothed saccular outgrowths in the gullet immediately behind the last gill arch" (Haedrich, 1967a, but see also Haedrich, 1967b).

Haedrich (1967a) recognizes only a single superfamily (including the Tetragonuridae).

SUBORDER XIPHIOIDEI.—Large oceanic fishes with 23–26 vertebrae and the anteriormost interneurals interdigitating between the cranium and the first vertebra; pelvic fins absent or reduced to three or fewer rays; pectorals inserted low on the sides; mouth inferior except in *Luvarus*. (Compiled.)

Superfamilies: Xiphioidae and Luvaroidae.

SUBORDER SCOMBROIDEI.—Vertebrae 30 or more; predorsal bones lacking; postorbital members of the circumorbital series of bones either fragmented or absent; upper jaw fixed except in *Scombrolabrax*. (Reworded from preceding account.)

Superfamilies: Scombroidae and Trichiuroidae.

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SUBORDER GOBIOIDEI.—"Parietals lacking. Branchiostegals (4) 5 or 6, the first one or two well separated from the others. Mesopterygoid narrow or absent. Preopercle and symplectic widely divergent above, with an interspace between them. Hypurals with a splint-like bone above and below" (Gosline, 1955, p. 166).

The Gobioidei generally have not been divided into separate superfamilies.

SUBORDER BLENNIOIDEI.—Pelvic fins, when present, inserted ahead of the pectorals; dorsal and posterior soft anal rays exactly equal in number to the vertebrae between them; caudal fin usually rounded. (Reworded from the preceding account.)

Superfamilies: Notothenioidae, Trachinoidae, Congrogadoidae, Blennioidae, and Zoarceoidae.

SUBORDER SCHINDLERIOIDAE.—Minute, transparent, neotenic, oceanic fishes with the last few vertebrae and the hypural fan fused into a single plate. (Compiled.)

This suborder contains only the genus *Schindleria*.

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TABLE 1.—*Families included under various classifications*

Jordan (1923) Order JUGULARES	Regan (1912d) Suborder BLENNIOIDEA	Fishes that will be included in the Blennioidei here
Series Trachiniformes		
Family Trachinidae		x
Series Notothenüiformes		
Family Nototheniidae		x
" Bathydraconidae		x
" Channichthyidae		x
" Bovichidae		x
" Harpagiferidae		x
Series Callionymiformes		
Family Draconettidae		
" Callionymidae		
Series Percophidiformes		
Family Percophididae		x
" Mugiloididae		x
" Parapercidae		x
" Pteropsaridae		x
" Hemerocoetidae		x
" Chimarrichthyidae		x
" Creediidae		x
" Limnichthyidae		x
" Trichonotidae		x
" Oxudercidae		x
Series Ammodytiformes		
Family Ammodytidae		
" Bleekeriidae		
" Hypoptychidae		
Series Bathymasteriformes		
Family Bathymasteridae		x
" Zaproridae		x
Series Uranoscopiformes		
Family Chiasmodontidae		
" Opisthognathidae		
" Owstoniidae		
" Champsodontidae		
" Uranoscopidae		x
" Leptoscopidae		x
" Dactyloscopidae	x	x

TABLE 1.—*Families included under various classifications*—Continued

Jordan (1923) Order JUGULARES	Regan (1912d) Suborder BLENNIOIDEA	Fishes that will be included in the Blennioidei here
Series Blenniiformes		
Family Clinidae	x	x
" Notograptidae	x	x
" Peronedyidae		?x
" Ophioclinidae	x	x
" Blenniidae	x	x
" Emblemariidae	x	x
" Runulidae	x	x
" Atopoclinidae	x	x
" Chaenopsidae	x	x
" Cebedichthyidae	x	x
" Pholidae	x	x
" Xiphisteridae	x	x
" Stichaeidae	x	x
" Lumpenidae	x	x
" Ptilichthyidae	x	x
" Cryptacanthodidae	x	x
" Anarhichadidae	x	x
" Anarrhichthyidae	x	x
" Xiphasiidae	x	x
" Xenocephalidae	?	?
Series Zoarciformes		
Family Congrogadidae	x	x
" Cerdalidae	x	
" Scytalinidae	x	?
" Zoarcidae	x	x
" Lycodapodidae	x	?x
" Derepodichthyidae		?x
Series Brotuliformes		
Family Brotulidae	x	
Series Ophidiiformes		
Family Rhodichthyidae	x	
" Ophidiidae	x	
Series Carapiformes		
Family Carapidae	x	
Suborder Haplodoci		
Family Batrachoididae		

TABLE 2.—*Basal characteristics*

ZOARCEOIDAE	NOTOTHENIOIDAE	Trachinoid-Blennioid-Congrogadoid Series
Tendency toward elongation	Tendency toward flattening of the head	Various, but the head usually not flattened
Tendency toward pelvic reduction	Tendency toward spread of pelvics with retention of 5 soft rays	Tendency to use the pelvics as props under the body with a strengthening of the outer rays and incision of the membrane between them
Tendency toward disintegration of circumorbital chain of bones	Tendency toward disintegration of circumorbital chain of bones	Tendency toward consolidation of circumorbital bones
Parasphenoid and frontals always form a stay excluding the prootic from the orbital border	Parasphenoid and frontals never form a stay excluding the prootic from the orbital border	Parasphenoid and frontals usually exclude the prootic from the orbital border
Basisphenoid never present	Basisphenoid usually present	Basisphenoid usually present
Medial extrascapular always fused with cranium	Medial extrascapular rarely fused with cranium	Medial extrascapular usually fused with cranium
Pectoral actinosts usually 4, broad	Pectoral radials 3 or 4, broad	Pectoral radials 4, variously shaped
All cold water forms	*Cold water forms* / *Tropical forms*	*All tropical forms*
One nostril on each side	One nostril / Two nostrils	Two nostrils

TABLE 3.—*Suborder Blennioidei*

Superfamily Notothenioidae
  Family Parapercidae (= Mugiloididae) (Cantwell, 1964)
    " Trichonotidae (sensu lato) (Schultz, 1960, except Cheimarrichthyidae)
    " Cheimarrichthyidae (Regan, 1913)
    " Bovictidae (Norman, 1957)
    " Nototheniidae (Norman, 1957)
    " Harpagiferidae (Norman, 1957)
    " Bathydraconidae (Norman, 1957)
    " Channichthyidae (Norman, 1957)
Superfamily Trachinoidae
  Family Trachinidae (Regan, 1913)
    " Uranoscopidae (Starks, 1923)
    " Leptoscopidae (Starks, 1923)
    " Dactyloscopidae (Starks, 1923)
Superfamily Congrogadoidae
  Family Congrogadidae (Regan, 1912d)
    " Notograptidae (Regan, 1912d)
  ? " Peronedyidae (Norman, 1957)
Superfamily Blennioidae
  Family Tripterygiidae (Hubbs, 1952)
    " Clinidae (Hubbs, 1952)
    " Chaenopsidae (Stephens, 1963)
    " Blenniidae (Hubbs, 1952)
Superfamily Zoarcoidae
  Family Bathymasteridae (Regan, 1913)
    " Stichaeidae (Makushok, 1958)
    " Pholidae (Makushok, 1958)
    " Anarhichadidae (Makushok, 1958; Barsukov, 1959)
    " Ptilichthyidae (Makushok, 1958)
    " Zaproridae (McAllister and Krejsa, 1961)
    " Cryptacanthodidae (Makushok, 1961a)
    " Zoarcidae (= Lycodidae) (Norman, 1957, in part)
  ? " Derepodichthyidae (Jordan and Evermann, 1898)
  ? " Scytalinidae (Jordan and Evermann, 1898)
  ? " Lycodapodidae (Jordan and Evermann, 1898)

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